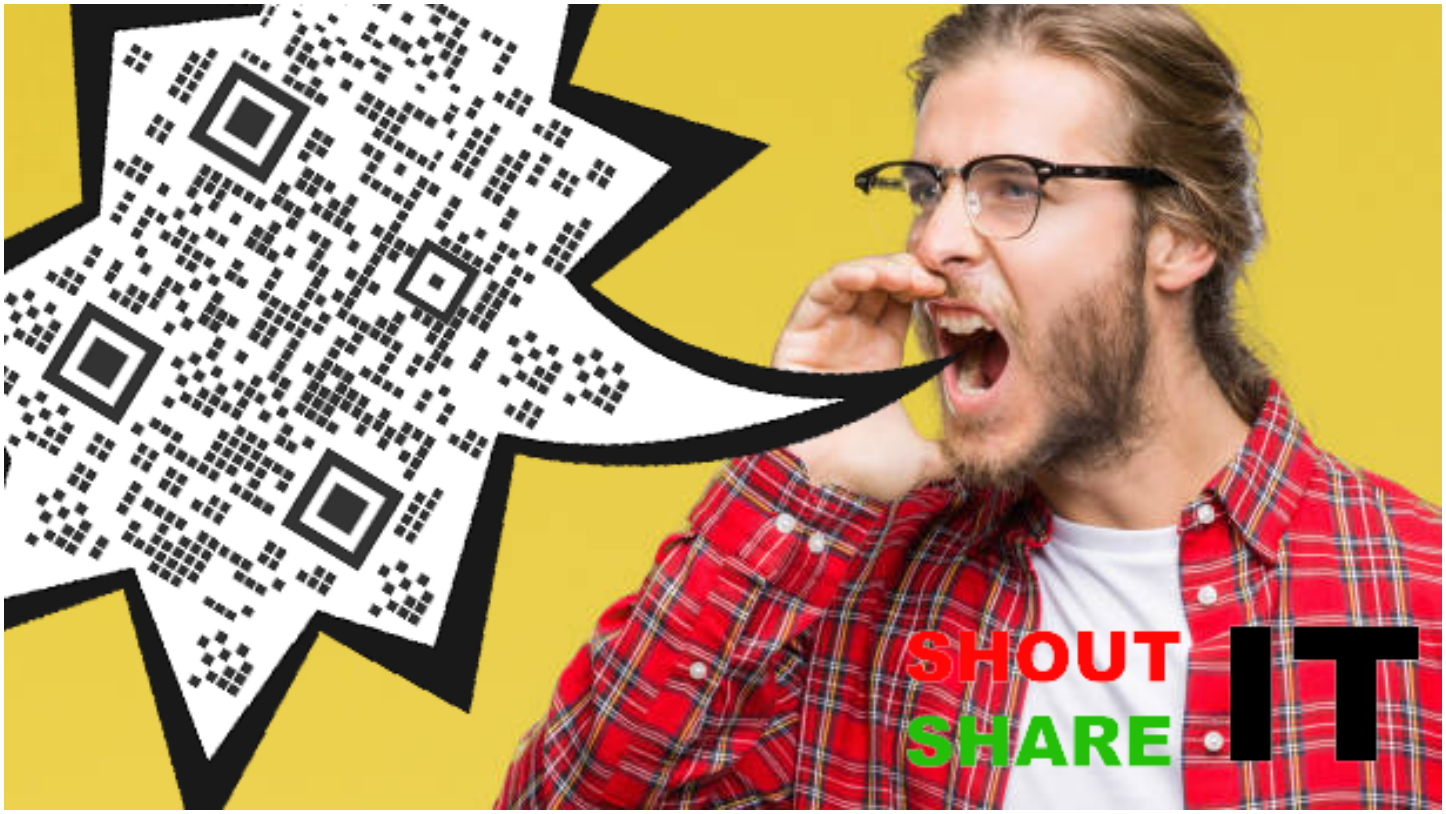
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MANUAL OF THE PENICILLIA

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A MANUAL
OF THE
PENICILLIA

BY

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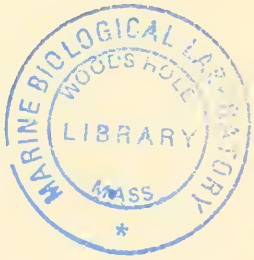

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PREFACE

Mycologically, *Penicillium* as the generic name of a group of green molds has been known for one hundred and forty years. Studies in this group were mainly floristic up to 1890. Green molds were everywhere and names for them appeared in every enumeration of the fungi of a particular locality, or of the species encountered in the study of decomposing or fermenting substances. Saccardo (1880) followed by Wehmer (1894, 1895) reported Penicillia active in the destruction of citrus fruit. Wehmer (1893) reported certain of them to be active producers of citric acid. Johan-Olsen (Sopp) (1898) related them to the cheese industry. The development of culture laboratories during this period made possible their isolation and examination in pure culture; and subsequent physiological studies led to increasing interest in their presence and significance.

Nevertheless, intensive study of the Penicillia was limited to less than a dozen laboratories, including those of Wehmer, Bainier, Sopp, Thom, Westling, Biourge, Zaleski, Van Beyma, and Raistrick, until the antibiotic penicillin was brought to America in 1941. Thenceforward, instead of individuals or small groups, hundreds of workers including bacteriologists, pharmacologists, chemists, and chemical engineers, turned their attention to the Penicillia. Instead of a casual academic pursuit, the identification of these organisms became a matter of prime biochemical and industrial importance. A restudy of the genus seemed urgent.

Thom's Monograph, *The Penicillia*, was published in 1930. In the intervening years, various new surveys have been made, many new species have been described, and biochemical investigations have directed special attention to many selected species. Finally the development of penicillin shifted the emphasis from single strains, often discussed as species, to the recognition of groups of variants bridging many of the gaps separating strains formerly given varietal or specific rank. Meanwhile, the accumulation of large numbers of strains, representing all of the major groups, made available sufficient material to support a systematic restudy of all of the Penicillia.

Upon the establishment of the Northern Regional Research Laboratory of the Bureau of Agricultural and Industrial Chemistry, U. S. Department of Agriculture, at Peoria, Illinois, the development of a collection of pure cultures of micro-organisms significant to agriculture and industry was undertaken. Raper, who had worked with Thom for the preceding decade, was transferred from the Laboratory in Washington to take charge, and brought with him cultures of all molds from the Thom Collection. Upon the retirement of Thom in 1942, all records and descriptive material ac-

cumulated by him at Storrs, Connecticut, and subsequently in the various laboratories in Washington which came under his direction, were transferred to Peoria. The Collection so established at the Northern Laboratory has been enormously increased during the past eight years by the isolation of new materials from many natural substrates, by the contribution of cultures by many collaborators, and finally through the cooperation of Dr. Johanna Westerdijk who, in 1946, contributed transfers of all of the Penicillia in the Centraalbureau at Baarn.

The first obligation of a monographer of the Penicillia is to report as truly as possible what his predecessors described under particular names. His ideal is to produce as complete and as faithful a presentation as possible of the work of his predecessors, supplemented by his own observations and knowledge. In contrast to the monographer, the writer of a manual of the Penicillia must begin with the establishment of a genus concept, then account for all species that have been assigned to it. He may correct, redescribe, reassign, or reduce to synonymy any specific name and description encountered, *so long as his own descriptions lead to the identification of actual material*, and to the assignment to that material of Latin names which are correct according to accepted rules of nomenclature. His primary obligation is to the investigator who needs to identify an organism. The manual must, in addition, furnish such guides to the literature as will permit the critical worker to search original sources for himself whenever he requires more detailed information than the manual supplies.

With this background and philosophy, the preparation of this Manual was undertaken. The monographic feature of Thom's earlier work (1930) has been dropped. The concept of series, i.e., groups of strains having fairly consistent morphology and usually showing related biochemical activities, is emphasized. Within each series, recognized species are arranged in what we consider to be a logical sequence, and the reasons for their recognition are indicated. The punctilious systematist will find that the description of a species of *Penicillium* is no longer a "photograph-like" presentation of the first strain, or type, as found, but represents instead a composite of characters selected as the result of continued cultivation of many strains. Such a concept is sufficiently broad and elastic to include the usual range of variants which the experienced worker will naturally expect. At the same time, we have attempted to establish species limits with sufficient clarity to exclude forms which are unrelated, and forms which may present only superficial evidence of relationship.

This Manual is designed primarily as a means for identifying Penicillia which may be encountered in the laboratory, or which for some reason may be significant in microbiological or biochemical processes. It is

hoped that it will minimize misunderstandings in the interpretation of species as described and understood by our predecessors. In addition, it is intended as a guide by which the investigator may reach the accumulated literature relative to the activities and significance of these molds.

Although the plans for this book had long been tentatively formed, and the materials partially segregated into fascicles, actual preparation followed the suggestion of Dr. W. J. Robbins, then Chairman of the National Science Fund, that help to speed up the completion of the book might be found. In the Spring of 1945 the George F. Baker Charitable Trust Fund made available to the National Science Fund a sum sufficient to provide the services of professional, technical, and clerical personnel necessary to carry out the work. Thereupon, a cooperative agreement was drawn up between the Department of Agriculture and the National Science Fund and work on the project was initiated in June 1945. The cooperation of the Northern Regional Research Laboratory in providing the time of the senior author, in supplying space and equipment, and in performing multitudinous administrative details has been essential to the completion of the task.

Since fully two thousand strains, in addition to our own original Collection of at least as many more, have been studied, it is impractical to recognize here the contributions of the many workers who cooperated by furnishing cultures. Acknowledgments are made in the text wherever their organisms are discussed.

In the preparation of this manuscript, and in the cultural studies upon which it is largely based, important contributions have been by May H. Flickinger and Jane A. Roberson who made cultures for examination and prepared lyophilized preparations of the strains discussed in the text; by Roland W. Haines and Robert E. Garrett, photographers at the Northern Regional Research Laboratory, who made all of the color pictures as well as the black and white photographs of plate cultures; and by Kathryn E. Dore who typed the manuscript in its final form.

The authors are indebted to the Chas. Pfizer & Co., Inc., Brooklyn, New York, for underwriting the cost of reproducing the natural color photographs.

Administratively, many individuals have contributed to the cooperative project under which this manuscript was prepared. These include W. J. Robbins and Harlow Shapley, Chairmen of the National Science Fund, O. E. May and L. B. Howard, Chiefs of the Bureau of Agricultural Chemistry and Engineering, and H. T. Herrick and G. E. Hilbert, Directors of the Northern Regional Research Laboratory.

THE AUTHORS.

PART I

GENERAL DISCUSSION

Chapter I

HISTORICAL

Species of *Penicillium* are so abundant and so conspicuous in all sorts of stale or decaying organic matter that they constitute a part of the common conception of mold, and are loosely referred to as "blue" or "green" mold. It is easy to guess, therefore, with Brefeld that some *Penicillium* furnished the material for *Aspergillus albus* in figure 3, table 91, of Micheli's "Nova Plantarum Genera" in 1729. Again, it is common mycological tradition that *Mucor crustaceus* of Linnaeus represented some *Penicillium*. This name passed from author to author thereafter without added information from real study of specimens. Persoon (1797, 1801) appears to have included the species in his conglomerate genus *Monilia*, again with very little evidence of study under higher magnifications. Some think that Linnaeus' species reappears in *Penicillium crustaceum* Fries (1829), but there is no continuity in materials and no evidence of real study. Saccardo, in the Sylloge in 1886 (Vol. IV, p. 78), went so far as to cite *Monilia digitata* Persoon as the basis of *P. digitatum*, although he furnished little proof of the continuity of this view even as tradition. Bulliard (1809) used the name *Mucor penicillatus* for these "broom" or brush-like forms and provided the first reasonably adequate illustration of a mold unquestionably representing a *Penicillium* (fig. 1).

The name *Penicillium* applied to a genus of fungi first appears in Link's "Observationes" (1809), in which he described very briefly the genus and three species: *Penicillium glaucum*, *P. candidum*, and *P. expansum*. Close scrutiny of these descriptions and all accessory information gives no clue to the identity of the molds which Link actually had under his microscope as *P. glaucum* and *P. candidum*, except that they presented the general appearance of the familiar penicillus or brush seen in the microscopic examination of Penicillia. *Penicillium expansum* was designated as the fruit rot which, in Berlin at that season, clearly pointed to the *Penicillium* rot of apples and related fruits (see Thom, 1930). We can, therefore, be reasonably certain of *P. expansum* Link as a recognizable generic type, world-wide in distribution. It is regrettable that Link, in 1824, abandoned his species *P. expansum* and called all the green Penicillia, *P. glaucum*. This practice has been followed by many workers to the present day with the result that use of the name *P. glaucum* now gives little clue to the real identity of a *Penicillium*.

Link's contemporaries, such as Persoon, Fries, and Greville (1823 to 1828), accepted Link's genus *Penicillium*, although their publications

give little evidence that any one of them actually knew which organism another had described under any of the different names proposed.

In *Penicillium*, as in *Aspergillus*, Corda (1837 to 1839) cleared up some of the uncertainties of structure evident in previous discussions of the genus, but his illustrations idealized the morphology of his species to such an extent that subsequent identification has never been satisfactory. Species of *Penicillium* are found described in the works of Bonorden, Fresenius, and Preuss during the period about 1850. These authors included with what we now call *Penicillium* such organisms as *Cladosporium*, *Hormodendrum*, or even *Monilia sitophila*. Few, if any, of the names they proposed can now be recognized as Penicillia. These workers represent a

FIG. 1. Bulliard's Plate 504, fig. XI, *Mucor penicillatus*. The earliest known figure unmistakably representing a *Penicillium*.

period in which the mycologist was primarily a microscopist, intent upon describing the specimens which came to hand either as fresh materials from his own environment or as herbarium specimens. A corollary to his work was the assumption that a mold found in any situation was sufficiently pure and characteristic to form a safe basis for taxonomic work. No cultures were made. The reactions of one organism to the presence of one or several others were not taken into account. The specimen was described, then labeled and dried for the herbarium, and the description was published whether or not the specimen was recognizable after it was so preserved. Montagne (1856) lamented that no one could find out what organism any of his predecessors used in describing their species, but he failed to offer a more efficient handling.

The same difficulty is encountered in interpreting the species of *Penicillium* described by Rivolta (1873), Berkeley (1841, 1875), Berkeley

and Broome (1881, 1882), Spegazzini (1895–1896), Cooke (1871 to 1891), and even Saccardo, all of whom were active, primarily as collectors, and brought to light many species of real value among groups which make more satisfactory herbarium specimens. The assumption that whatever was found in nature undisturbed by man was normal early became dominant and still persists in much of the taxonomic literature.

Many years were required for mycologists to realize that among these molds, much of what we now loosely call morphology, represents response to environment. For example, a mold grown in the presence of a fermentable sugar may show one aspect; whereas, the same mold, if grown on a leather shoe or some other nitrogen-rich substrate, may assume a very different appearance. If grown in mixtures with other molds and bacteria, the colonies of a particular culture often lose identifying characters based upon its development in some other environment. Thus, the idea of growing molds in pure culture under standardized conditions as a basis for taxonomy gradually developed.

DeBary's laboratory began to report work with cultures of molds between 1850 and 1860. It was not, however, until Brefeld published the life history of "*Penicillium glaucum*" in 1874, that real cultural study of the Penicillia was initiated. He limited the discussion to one species, *P. glaucum*, which is nowhere in his paper fully described, although structures encountered at each stage of its life history were described in detail and elaborately figured. Part of these figures show evidence of being drawn from actual preparations; others are obviously schematic and present Brefeld's interpretation of his observations. The method of conidium formation was evidently not understood, but the general structure of the penicillus was beautifully developed. The formation of perithecia as hard sclerotium-like masses of pseudoparenchyma, followed by the slow development of ascogenous central areas, was described and illustrated, although such were not to be unmistakably reported again until the studies of Dodge (1933), van Beyma (1929, 1933), and Shear (1934), more than fifty years later. Brefeld states that he was working with the "common *P. glaucum*," which is generally interpreted as approximating *P. expansum* Link as we know this species today. His work was done with the cruder methods of culture which preceded the rise of bacteriology with its provision for protecting cultures against contamination, hence it is not surprising if the various drawings presented suggest the probability that more than one species was involved in his series of cultures. One of his figures, depicting a coremium from a rotting pear, apparently represents some strain of *P. expansum*; and the figures of some of his penicilli closely approximate this species except that conidia are generally elliptical (fig. 7B) rather than globose as shown in Brefeld's figures (fig. 2). The peri-

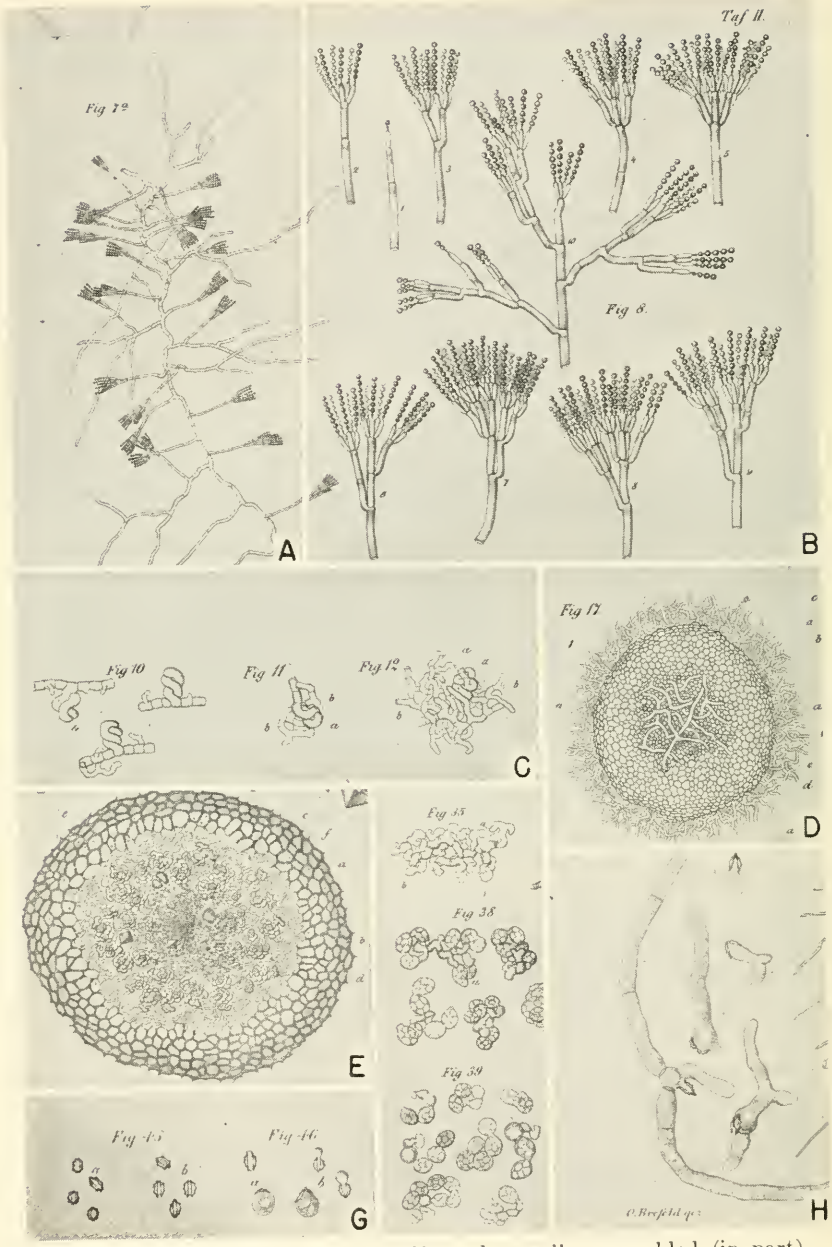


FIG. 2. Brefeld's figures of *"Penicillium glaucum"* reassembled (in part). *A*, Habit sketch showing origin of conidial structures, × 75. *B*, Detailed drawings of penicilli, × 400. *C*, Initial stages in perithecium formation, × 400. *D*, Young perithecium with fertile ascogenous hyphae beginning to appear, × 175. *E*, Mature perithecium containing asci and ripe ascospores at center, × 175. *F*, Developing asci showing their characteristic origin in chains, × 400. *G*, Mature and germinating ascospores, × 500. *H*, Germinated ascospores, × 500. (After Brefeld, 1874.)

thecia as described and illustrated, both in form and development, approximate those seen in strains now assigned to species in the *Carpenteles* and *P. javanicum* series (fig. 2). Other of his penicilli might belong to some species such as *P. egyptiacum* van Beyma, or possibly *P. asperum* (Shear), in which case they might easily have developed upon the same mold that produced the sclerotioid perithecia with tardy ascospore formation. His ascospores, with equatorial ridges and rough side walls, could have belonged to some species such as *P. asperum* or *P. baarnense* van Beyma. No one can be certain whether Brefeld worked with a mixture of two species; or whether he worked with a single *Penicillium*, and some of his drawings (obviously schematic) are misleading; or whether he worked with a single strain and illustrated it accurately throughout. We can say, however, that no single species is known to us which combines all of the characteristics illustrated by Brefeld. When one considers the level of laboratory culture techniques of his day, and the state of mycological knowledge then existing, one cannot but admire the skill and care exhibited in his work.

The use of the name *Penicillium glaucum* for the apple-rot organism was continued in Sopp's Monograph (1912, p. 48) and in Wehmer's Beiträge (1893). Both men were students in Brefeld's laboratory, hence the continuity of this usage is evidence of an understanding among them that this organism should be regarded as *P. glaucum*.

Wehmer, in 1895, published his studies of the Penicillia occurring upon rotting fruit. He figured and described the destructive effects of *Penicillium expansum* on apples, pears, and grapes—but under the name *P. glaucum*. The olive colored rot of oranges, already described by Saccardo as *P. digitatum* in 1880 and distributed in Mycotheca Italici, was called *P. olivaceum*, and the soft rot organism with blue-green colors was correctly regarded as new and named *P. italicum*. In the same year he published his study of citric acid-forming molds, to which he gave the name *Citromyces*, and his study of ascospore formation in *P. luteum* Zukal. Wehmer was the first investigator to pay particular attention to the physiological and biochemical activities of molds, and he prepared the studies of this group in the second edition of Lafar's Technische Mykologie (1906).

Sopp[1] records that he recognized as early as 1890 that the name *Penicillium glaucum*, in addition to designating the apple rot organism, was being used to cover more than a single species. Elfving came to the same conclusion in 1895. In 1898, Sopp separated certain of the forms found active in cheese ripening as *P. aromaticum*. Unfortunately his descriptions of these organisms were entirely inadequate, apparently depending for identification primarily upon their presence upon particular varieties

[1] Early papers signed Olav Johan-Olsen.

of cheese. Even in his Monograph (1912) this usage remains too indefinite to be verified. His Monograph brought together a mass of descriptive matter and many figures covering some sixty species of *Penicillium*, together with descriptions and illustrations (some colored) of forms which he thought to be closely related. Despite the mass of data presented, very few of his species have been identified with certainty by other workers. Insofar as we know, he never distributed any cultures.

Dierckx published his "Essai" in 1901, in which he sketched his method of work and proposed a series of twenty-five new species with descriptions so brief and inadequate that no one working with the published material succeeded in identifying any of his new species. As noted by Saccardo in the Sylloge, the new names proposed were not supported by descriptions or figures which would identify them. He appears, however, to have left in the laboratory at Louvain, colored plates, descriptive material, and sufficient of his cultures to enable Biourge to reidentify and redescribe twenty-two of these forms in 1923. Biourge obviously based his recognition and perpetuation of some of Dierckx's specific names upon the accessory material left by Dierckx.

Thom began to study Penicillia in connection with cheese investigations in 1904, published "Fungi in Cheese Ripening" in 1906, his "Cultural Studies of species of *Penicillium*" in 1910, and his group concept of classification of the Penicillia in 1915. In these papers the necessity of comparative culture upon standardized media was stressed in contrast to the search for optimum conditions of culture, organism by organism.

Weidemann in Kiel (1907) and Westling in Stockholm (1911) used careful cultural methods in describing their series of green Penicillia. But neither worker had a large enough collection, nor followed the study long enough, to determine group relationships.

Bainier, under the general title "Mycotheque de l'Ecole de Pharmacie" (Paris), began publishing descriptions of species of *Penicillium* in 1905 and continued partly separately, partly with Sartory, until 1914. In this series of species many forms were described and figured with meticulous care, hence some of them are readily identified. Efforts were made to maintain all of these forms in culture at l'Ecole de Pharmacie. Bainier separated the form described later by Thom (1910) as *Penicillium divaricatum* and made it the type of his genus *Paecilomyces* (1907). He also designated *P. brevicaule* Saccardo, with its numerous allied forms, as the basis of a new genus, *Scopulariopsis* (1907). The separation of both of these groups from *Penicillium* can be readily justified upon the ground of lack of essential relationship. Bainier adopted Wehmer's genus *Citromyces* and described his monoverticillate strains as species under that name.

Biourge, under the stimulus of Carnoy, began to study Penicillia in

1897. After Dierckx published his "Essai," Biourge took up the task in earnest. He gave a brief survey of this work in a conference at Louvain in 1916, which was published as a pamphlet in 1920, followed by his Monograph in 1923. In this latter work, Biourge followed along the culture lines already proposed by Dierckx, broadened his work to cover most of the studies made by Thom, and gave a brief Latin diagnosis for some 125 species, followed by culture notes in French. The descriptions were supplemented by line drawings of the conidiophore, penicillus, and conidia, and colored plates showing the colors and color changes of his colonies. It represented, beyond question, the most comprehensive and elaborate study of the genus made up to that time.

Unfortunately Biourge's microscopic work was largely done from fruiting structures removed from cultures preserved in alcohol. Furthermore, he paid little attention to the colony habit with its large contribution to our knowledge of the organism as it grows in the culture tube or petri dish. In the main, Biourge had a fairly good idea of the group relationships within the genus *Penicillium*, and certain of his divisions are tangible enough entities. His Radiata, covering what we now recognize as the *Penicillium chrysogenum* series, is illustrative.

Biourge's conception of the genus in the broadest sense called for the inclusion not only of *Coremium*, *Citromyces*, and of more or less related series like *Scopulariopsis*, *Gliocladium*, and *Paccilomyces*, but part or all of several other genera in which figures or descriptions offer suggestions of a penicillate conidial apparatus.

Zaleski (1927) described as new thirty-five species and one variety of *Penicillium* from the forest soils of Poland. His descriptions go into unnecessary detail regarding the buckling and wrinkling of colonies upon gelatin, as the substratum becomes liquefied. Methods of microscopic observation followed Biourge to the destruction of much useful information regarding the structure and appearance of the conidium-producing organs as they are developed in the colony. His cultures and notes were sent to Biourge whose comments are given for certain species, but whose opinions were not always followed. In the main, however, he accepted the subgenus, section, subsection, and series divisions as given in Biourge's Monograph and fitted his species into this scheme insofar as possible. He apparently confined his study to the soil organisms which he isolated, hence had no background of comparative knowledge of the many cosmopolitan saprophytes already recognized as belonging to the genus. Careful comparative study has tended to reduce most of his species to synonomy with other species previouly described.

Thom, in his comprehensive Monograph, brought together all of the material on the taxonomy of *Penicillium* published up to that time (1930).

He stressed the importance of description from cultures grown in the laboratory under uniform conditions and emphasized the importance of observations made on the growing colony and developing conidial structures. He emphasized further the group concept of classification which he had developed over a period of years. Species which had been described in adequate and tangible terms, or which were based upon living cultures that could be used as reference material, were for the most part recognized. In presenting these, the describer's species diagnosis was usually supplemented with Thom's own observations, together with pertinent remarks regarding the probable relationships of the form. Species which were unrecognizable because of inadequate description were so labeled but likewise included, and, wherever possible, notations were made as to their possible relationships. *Paecilomyces*, *Gliocladium*, and *Scopulariopsis* were separated from *Penicillium* but treated as related genera. Whereas this work was primarily monographic in character, the biochemical and physiological activities of the Penicillia as a whole were summarized and reported for the first time.

In the years since 1930, George Smith and G. E. Turfitt, of the London School of Hygiene and Tropical Medicine, and F. H. van Beyma, formerly at the Centraalbureau in Baarn, Holland, have added substantially to our knowledge of the Penicillia. All have contributed new and valid species to the genus. The species of these authors have been fully and carefully described, and with few exceptions, are accepted in this Manual.

Armin von Szilvinyi, working in the Biological Station at Lunz under the supervision of the "Institut für Biochemische Technologie an der Technischen Hochschule in Wien," in 1941 described a series of Penicillia, mostly obtained in the neighborhood of Lunz. Only a few of the cultures used have found their way into the Centraalbureau or other well-recognized collections, hence they have been unavailable for study. Von Szilvinyi apparently believed that identification with a particular local environment amply justified taxonomic recognition. A few species were described as new, but most of his isolates were accorded a varietal rank (var. *lunzinense*) and assigned to species already described. Little basis exists for most of these varieties, hence they must be referred to the species named, or to other species when critical study of his data demands the change.

In describing species that he believed new, he left out important data such as the origin and length of the conidiophore and failed to include significant observations on the penicillus as it appears in petri dish culture under low magnifications of the compound microscope. The deficiencies in his descriptions and illustrations, together with the inaccessibility of his organisms in culture, make placement of most of these species

little more than guesses. Such species and varieties will be found only in the Species Index (Chapter XVIII).

Following Brefeld's work, Zukal, in 1889, described *Penicillium luteum* as an ascosporic form with the unmistakable conidial apparatus of a biverticillately symmetrical *Penicillium*. Asci were borne throughout a loose network of hyphae almost if not completely lacking a perithecial wall. From that description, Saccardo, without examining material (Sylloge **11**: 437. 1895), transferred the species to *Gymnoascus*, as *G. luteus* (Zukal) Saccardo. Zukal described elliptical ascospores ornamented with a spiral band passing 2 to 3 times around the cells. Wehmer (1893) clearly illustrated the same type of spore. For many years thereafter no one found such an organism in culture, although many related organisms were collected. Derx (1925–1926) reported having had one. Professor Bisby sent one to us from Manitoba in 1933, which was included in Emmons' study of the ascocarps in *Penicillium* (1935). One or two others have been seen. Subsequent to Zukal's description of *P. luteum*, other workers, including Klöcker (1903), Dangeard (1907), Thom and Turesson (1915), Lehman (1920), Emmons (1935), Swift (1932), and Raper and Fennell (1948), reported a number of ascosporic Penicillia showing the general series characteristics of Zukal's species but differing in specific details.

Examination of organisms identified as species of *Gymnoascus* reveals ascogenous structures closely related to the *Penicillium luteum* series. Detailed search through colonies of certain species of *Gymnoascus* discloses very simple penicilli consisting of short conidiophores and groups of one, two, or rarely more sterigmata bearing chains of conidia. One is compelled to believe that *Penicillium* and *Gymnoascus* come very close to each other, morphologically, in the *P. luteum* series.

In another series, typified by *Penicillium javanicum* van Beyma (1929), the perithecium first develops as a pseudoparenchymatous mass of polyhedral, thick-walled cells at the center of which an ascogenous core subsequently arises, and by enlargement gradually comes to occupy the entire body except for a firm wall or peridium few to several cells in thickness. Other monoverticillate species with perithecia of this same general character have been described by Klebahn (1930), Dodge (1933), and Raper and Fennell (1948). The same process of perithecial development occurs in the *Carpenteles* series noted above, but the penicilli in these latter forms are typically biverticillate and asymmetrical, and the forms are placed in the Divaricata.

Langeron (1922), on purely bibliographic grounds, created the genus *Carpenteles* for Brefeld's *Penicillium glaucum*, but since he studied no cultural material the genus went unaccepted until Shear (1934) attached it

to an organism which he believed to represent Brefeld's strain. He proposed to move all of the forms producing hard-walled perithecia out of *Penicillium* into *Carpenteles*. Van Beyma (1933) accepted the change with some reservations, but for adequate reasons others have not cared to disinter Langeron's generic usage. Such transfer is illogical and constitutes a basis for unnecessary confusion, for strains maintained in the laboratory may quickly lose their ascospore-producing power. The same strain, when first picked up out of doors may be readily identifiable as *Carpenteles*, only to later have to be referred to the genus *Penicillium* when perithecia are no longer developed. The transfer of a small fraction of a great group of obviously related organisms to a new genus because an occasional strain produces ascospores, seems to us a fantastic interpretation of the rules of nomenclature. Enough has been said to show the background of our conclusions that the cause of a permanent nomenclature is better served by emending Link's inadequate diagnosis of the genus *Penicillium* to include the citation that some series in the genus produce asci, than by recognition of any separate name or names for the ascospore producers. This course is likewise supported by historical considerations since Brefeld (1874), Zukal (1889), and others described ascosporic forms as species of *Penicillium*.

The series with firm perithecia seem to pass directly into forms producing sclerotia, from which a potential ascogenous center has possibly been obliterated. No one has found it possible to obtain asci from proved sclerotium producers, although morphologically these may be quite similar to other strains found in nature as perithecium and ascus producers.

In summary, the authors are fairly familiar with accepted rules of nomenclature, and are intimately acquainted with the literature of *Penicillium*. More important, we have had first hand cultural experience with thousands of strains of Penicillia in comparative cultural studies, and representing the whole range of morphology in the group. We believe that the system of nomenclature to be followed in a Manual of this type should combine due consideration of the views of our predecessors with the presentation of a workable system of descriptive diagnoses which will enable the user to identify the molds he has in culture. With this ideal in mind we apply the generic name *Penicillium* to the whole group of strictly penicillate green molds, with or without ascospore production. Variant, or mutant strains or species in which the factor for green or blue-green color is not evident are retained in *Penicillium*, as are also all other mutant types developed from parent strains clearly representing members of the genus *Penicillium*.

Gliocladium of Corda is used for a group in which the general branching of the conidial apparatus simulates that of *Penicillium*, but in which the

sterigmatic cells taper gradually toward a narrow tube, in which the conidia are consistently elliptical, and in which the maturing cells become enveloped in slime. No ascosporic stage is known.

The brown or yellowish group with a conidium-producing tube set at an angle to the principal axis of the sterigmatic cell is separated, following Bainier, as *Paecilomyces*. The ascosporic stage associated with this type of mold is assignable to Westling's genus *Byssochlamys* (1909).

Scopulariopsis of Bainier is accepted for a morphologically consistent series in which the conidia are characterized by a more or less conspicuous basal ring surrounding a germinal pore. Conidial areas are generally in some shade of brown, avellaneous, yellow, or more rarely cream or white, but *never* green. Conidia are borne upon long narrowly tapering sterigmata in more or less penicillate aggregates. Perithecia when present are black walled, ostiolate, and do not resemble those of known Penicillia; they are assignable to Zukal's genus *Microascus* (1885).

Close genetic relationship of these genera to *Penicillium*, particularly *Paecilomyces* and *Scopulariopsis*, is not assumed. Nevertheless, since they do produce conidial structures more or less penicillate, and since the literature of these forms is inextricably interwoven with that of *Penicillium*, we regard some consideration of these genera as mandatory. They are briefly reviewed in a separate chapter following our discussion of the different sections of the genus *Penicillium* (see Chapter XV).

Chapter II

GENERIC DIAGNOSIS AND SYNONYMY

Class: Ascomycetes
Order: Plectascineae
Family: Aspergillaceae
Genus: *Penicillium*

Class: Fungi Imperfecti
Subclass: Hyphomycetes
Order: Mucedineae
Family: Mucedinaceae
Subfamily: Aspergilleae
Genus: *Penicillium*

In the first of the above schemes *Penicillium* is included among the ascosporic fungi where we believe it rightfully belongs. This preferred classification follows Engler and Prantl (1897).

The genus is likewise considered among the Hyphomycetes to facilitate the identification of species for which no ascosporic stage is known. Since the latter forms far outnumber those which produce perithecia, a successful taxonomy of the genus *Penicillium* must be based upon an orderly arrangement of these asexual types. Nevertheless, it is our firm belief that the genus concept should be sufficiently broad to include ascosporic organisms which produce conidial structures, or penicilli, unmistakably similar to those of strictly conidial strains and species. Recognition of separate genera, such as Langeron's *Carpenteles*, to include forms producing perithecia is unnecessary and unjustified.

Changes in the names of class, order, and family may appear in other proposed systems, but usually without significant differences in placement.

Generic Diagnosis

By common consent the generic name *Penicillium* proposed by Link in 1809 was promptly accepted for Hyphomycetes producing conidial fructifications in the form of a brush or broom called by the Latin term, the penicillus. Link failed to specify the components of the penicillus, hence the name has been loosely applied to almost every mold having a conidial apparatus suggestive of such a brush or broom. Since the application of the name has often rested upon superficial resemblances rather

than actual homologies, members of several different genera have, from time to time, been given specific names as Penicillia.

Link included three species, namely: *Penicillium glaucum*, *P. candidum*, and *P. expansum*. Thom, in conference with Shear (Thom, 1910), concluded that *P. expansum* could be accepted as the type species for the genus since it was represented by known material in the form of the apple rot *Penicillium*.[1]

With cultures of *Penicillium expansum* thus representing the nearest verifiable approach to Link's material, Thom (1910, 1930) felt justified in emending Link's generic description to include a fairly homogeneous group of series and species, and equally to exclude other types, or aggregates. In doing so it became essential to recognize that in certain series asci were produced by species or strains morphologically indistinguishable in their conidial forms from strains which failed to produce asci. Following the position earlier taken by Thom, the authors of this Manual believe that the whole complex aggregate can best be covered by an emended generic description of *Penicillium*.

We are fully aware that different workers since Link's time have assigned to *Penicillium* species showing conidial fructifications that present or suggest a penicillate arrangement without attempting to analyze the morphology of the conidial apparatus, or to give any reason other than the suggestion of a brush or broom (the penicillus). We wish to emphasize also that Brefeld called his ascosporic form *Penicillium*, and did not fabricate a new generic name because a mold that he believed to be a known *Penicillium* produced ascospores. With a century and a quarter of Penicillium literature before us, we see no alternative but to use the name *Penicillium* for both ascosporic and conidial forms unless and until it is shown that seriously discordant elements would be included. *Gliocladium*, *Scopulariopsis*, *Paecilomyces*, *Byssochlamys*, and perhaps some other forms which have at times been assigned to *Penicillium*, are readily excluded by their conidial fructifications or ascosporic apparatus. Our emendation of the generic diagnosis follows:

Penicillium Link, in "Observationes," p. 17. 1809; emended, Thom, in the U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, pp. 27–28. 1910; also Thom, The Penicillia, pp. 8–9. 1930.

Vegetative mycelium abundant, entirely submerged or more or less effused, monopodially branching, septate, commonly showing vegetative anastomoses, colorless or secondarily colored by products of metabolism

[1] The bases for accepting *Penicillium expansum* Link as the type species for the genus were discussed in greater detail by Thom in 1910 and 1930.

which frequently also discolor the substratum, never with hyphal walls brown or dematiaceous; colonies green, yellow-green, blue-green, gray-green, or less commonly colorless or in avellaneous to yellow, reddish, purplish, or other shades, frequently discolored in age even with spores brown in mass, but not dematiaceous; fertile hyphae or conidiophores arising as branches from the vegetative mycelium, frequently perpendicular to the vegetative hyphae, but not showing differentiated foot-cells as in *Aspergillus*, with walls in some forms smooth or undifferentiated, in others more or less conspicuously roughened from secondary thickening, not dematiaceous; conidial apparatus forming a brush or broom, the penicillus, ranging from a single terminal verticil of conidia-bearing cells or sterigmata, or, a terminal verticil of equal branches or metulae bearing verticils of sterigmata, to complex branching systems ending in verticils of specialized cells or metulae bearing verticils of sterigmata; sterigmata bearing *single unbranched chains* of conidia each cut off from the tip of an apical, straight, conidium-bearing tube; conidia cylindrical to elliptical, oval, or globose, smooth or roughened, colorless or variously colored, especially in mass, but not dematiaceous. Sclerotia produced in some series and species, not in others; composed of thick-walled cells, usually hard and somewhat brittle or horny, but in a few species comparatively soft. Perithecia characteristic of some species, not of others; varying markedly in texture, in some species soft, loose-textured, quickly developing asci and ascospores throughout, in other species firm to hard, pseudoparenchymatous, ripening from the center outward and often tardily.

Other Genera to Which Penicillia Have Been Referred

Many different genera appear in connection with the literature of *Penicillium*. Some of these were established to include limited portions of the genus as we now know it, hence should be regarded as synonyms. In others, conidial structures more or less penicillate in character oftentimes or regularly occur, hence species correctly assignable elsewhere have commonly been described as Penicillia. Observations or views that are believed to be pertinent regarding the different usages are noted. Since there is no significant connection between most of the names involved, the various proposals are presented alphabetically:

Acaulium Sopp, in Monogr., p. 42. 1912. Type species: *Penicillium brevicaule* Saccardo.

Synonym: *Scopulariopsis* Bainier, in Bul. Soc. Myc. France **23:** 99–103, Pl. XI, figs. 1–6. 1907.

Sopp's description of the above added nothing to the characters of the well known fungus *Penicillium brevicaule* Sacc. In certain of his species

of *Acaulium* Sopp reported perithecia which showed well defined ostioles, but stopped short of adequate descriptions of asci and ascospores which would have insured subsequent recognition of his species by these characters. More recently Curzi (1930), Emmons and Dodge (1931), and Jones (1936) have reported similar perithecia for species of *Scopulariopsis*, with which genus Sopp's *Acaulium* is regarded as synonymous.

Aspergilloides Dierckx, in Soc. Scien. Brux. **25:** 83–89. 1901.

Dierckx used this name to include species now assigned in the monoverticillate section of *Penicillium*.

Aspergillopsis Sopp, in Monogr., pp. 201–202, Taf. XX, fig. 149 and Taf. XXIII, fig. 31. 1912.

This generic name was proposed for Penicillium-like forms in which the stalk, or conidiophore, ended in a globose or clavate apex producing pear-shaped or clavate "sterigmata" (or metulae?) radiating in all directions. Each "sterigma" (or metula) bore a verticil of 5 to 15 short, thick cells producing conidial chains. Sopp regarded this group more as presenting transitional forms toward *Penicillium* than toward *Aspergillus*. He described one species, *A. fumosus*. The genus may as well be dropped since no authentic material has been reported since the genus was described.

Byssochlamys Westling, in Svensk Bot. Tids. **3:** 134, Taf. 4. 1909.

Generic diagnosis: Mycelium floccose, white, hyphae prostrate, plurinucleate; asci abundantly produced, naked, almost sessile; 8-spored, in clusters without perithecial walls. Chlamydospores formed from the tips of the hyphae, solitary; conidia in chains, with sterigmata short and mostly borne singly. The genus was described as intermediate between the Endomycetaceae and the Gymnoascaceae.

Westling's culture (*Byssochlamys nivea*) has not been seen, but Olliver and Smith (1933) described *Byssochlamys fulva* to cover a strain with the conidial morphology of a *Paecilomyces* in which structures believed to be homologous with the chlamydospores of some authors, or the macrospores of Horne and Williamson (1923), became asci.

Carpenteles Langeron, in Compt. Rend. Soc. Biol. Paris **87:** 343–345. 1922.

Langeron proposed *Carpenteles* as a new genus to include ascosporic Penicillia, naming *Penicillium glaucum* (Link) Brefeld as type. His proposal was unsupported by investigations, hence acceptance must be withheld unless someone supplies sufficient data to make the genus useful. Shear (1934) assigned an ascosporic *Penicillium* to this genus as *C. asperum*

and proposed to move into *Carpenteles* all Penicillia producing sclerotioid perithecia which tardily develop asci. Very few workers consider the suggested changes desirable at present.

Citromyces Wehmer, in Beitr. z. Kennt. einh. Pilze I, pp. 1–92, Taf. I and II. Hannover and Leipzig, 1893. Discussed by Westling, Arkiv för Bot. **2:** 41. 1911; by Sopp, Monogr., p. 184. 1912; by Thom, U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, p. 23. 1910; and The Penicillia, 1930; and Biourge, Monogr., La Cellule **33:** pp. 32, 265, 331. 1923.

Wehmer proposed to separate into the genus *Citromyces*, penicillate species in which conidiophores originated as branches of vegetative hyphae and developed a vesicle-like swelling at the apex upon which a single verticil of sterigmata was produced. The sterigmata did not differ from those of typical Penicillia, and unbranched chains of conidia were produced. No perithecia were described, but aggregations of hyphae suggestive of some form of fruit body were mentioned in the description of *C. pfefferianus*. The forms under observation by Wehmer produced citric acid by the fermentation of sugar solutions, hence the name. Citric acid production has been shown by Tiukow (1931) and others to be a very general biochemical activity among several groups of molds rather than a particular characteristic of these species. The arguments for the name are not convincing.

All efforts to obtain the exact strains used in describing Wehmer's two species failed, although the general morphology represented is readily found in many forms in our Collection.

Species of *Citromyces* have been described by Sopp (1912), Bainier and Sartory (1912, 1913), Maźe and Perrier (1904), Pollacci (1916), and mentioned or discussed by many others, especially in connection with biochemical or technological studies. No one, however, can collect a large number of these organisms without finding that every gradation from the conidial apparatus of *Citromyces* to *Penicillium* may be found. Among forms obviously nearly related, some might easily fall in one genus, some another. Thom (1930) followed Biourge in dropping the generic name.

Clonostachys Corda, in Prachtflora, p. 31, Taf. XV. 1839. Type species: *C. araucaria* Corda.

Corda's diagnosis included: Mycelium creeping, continuous (?); stalks erect, simple, continuous, verticillately branched above; each branch bearing 2 or more superimposed verticils of 4 sterigmata each at successive nodes; sterigmata (ramuli) subulate with apex subcapitate, bearing spores spirally, forming a kind of spike; spores unicellular, with walls hyaline and contents curved around a central globule.

Corda's figure and description have been interpreted as covering certain fruiting forms occasionally encountered. We have had several cultures showing a penicillus-like structure in which the column of conidia assumed the appearance indicated by Corda's figures, but the branching system lacked the definite verticils of 4 sterigmata at each node prescribed by Corda. They did, however, reproduce the figure of *Penicillium roseum* as given by Thom, 1910, which were subsequently recognized as representing a *Gliocladium* (Thom, 1930). In fact, many observations suggest that the rosy or salmon forms which may show a penicillate condition at one stage, a Gliocladium-like fruit at another, and again *Clonostachys* heads upon the same mycelium, should be restudied and some usage devised which will indicate the real relationships involved. Other names should be reduced to proper synonymy.

Coremium Link, in "Observationes," p. 19. 1809.

Link described *Coremium glaucum* on p. 19 after describing *Penicillium expansum* on p. 17 of his "Observationes." Comparative study of decaying fruit has led us to believe that *C. glaucum* was the coarsely coremiform development that we now know to occur from the growth of *P. expansum* upon such fruits as apples in storage. The name has continued to be loosely applied by some to coremiform fruiting masses wherever found. The generic name *Coremium* is, therefore, commonly listed among the Stilbaceae. We can see no purpose in using the name for any known Penicillium-like organisms.

Corollium Sopp, in Monogr., pp. 98–103, fig. 108. 1912. See also Olav Johan-Olsen (Sopp) in Pharmacia, No. 22 and 23. 1904.

Probable synonym: *Paecilomyces* Bainier, in Bul. Soc. Myc. France **23:** 26–27, Pl. VII. 1907.

Sopp's generic description can scarcely be separated from that of his type species, *Corollium dermatophagum*. *Corollium* is reported to be most nearly related to *Acaulium* but to connect with the true Penicillia through *Penicillium olivaceum* and *P. italicum*. It appears upon moist leather as a clear brown to yellow-green, close felted mycelium becoming powdery or mealy in age, with conidial masses of the penicillate type borne at the apices of fertile hyphae, but accompanied by abundant verticils of sterigmata broadly and irregularly distributed on the fertile hyphae. The type species of this genus was found upon a pair of old boots in a military depot in Norway. It grows readily upon a wide range of media and is thermophilic.

Dactylomyces Sopp, in Monogr., pp. 33, 35–42, fig. 20; Taf. IV, figs. 21–30. 1912. Type species: *D. thermophilus* Sopp.

Probable synonym: *Thermoascus* Miehe (1907).

Sopp's diagnosis hinged on the following items: Conidiophores bear finger-like branches at the apex, each enlarging to a vesicle-like apex, suggestive of the basidia of *Tomentella*, these branches produce similar secondary verticils and such branching may be repeated three, four, or more times, hence the name *Dactylomyces*, perithecium formation begins quickly and the cycle from ascospore to ascospore requires only a few days. Aside from the general resemblance of the perithecium to that of certain Penicillia and the rough similarities of the conidial apparatus, the true affinities of the organism studied by Sopp are difficult to determine.

Professor Ralph Emerson, studying the retting of guayule shrub at Salinas, California reisolated a strain believed to represent Sopp's species and sent it to us. Conidial structures are very large and coarse, evanescent, but somewhat penicillate. Perithecia are strongly suggestive of those seen in *Penicillium vermiculatum* and *P. wortmanni* but larger; ascospores are quite large, elliptical, echinulate. The species is thermophilic.

Eidamia, in Horne and Williamson, Ann. Bot. **37:** 393–432, figs. 1–13. 1923

These authors assigned two new species to Lindau's genus *Eidamia*. One of these, when examined, proved to be a common *Trichoderma* and the other some strain of *Paecilomyces*. Assignment to *Eidamia*, unjustified in either case, was in the latter instance based largely upon the production of enlarged, more or less heavy-walled "macrospores" which were either terminal or intercallary.

Eupenicillium Ludwig, in Lehrb. niederen Krypt., pp. 263–265. 1892. Stuttgart.

Ludwig merely accepted Brefeld's discussion of *Penicillium glaucum* and made it the basis of a new ascomycetous genus, *Eupenicillium*. His discussion was headed, "Der gemeine Pinselschimmel, '*Eupenicillium crustaceum* (L.) Fr. (*P. glaucum*)'", and consisted of an abstract of Brefeld's discussion of *P. glaucum* with the generic name changed to *Eupenicillium*. Ludwig offered no real contribution to our knowledge of the genus and his proposals have been justly ignored by most workers.

Gliocladium Corda, in Icones Fungorum **4:** 30–31, Taf. VII, fig. 92. 1840. Type species: *G. penicilloides* Corda, *ibid.* Latin description repeated

in Icones **5:** 14. 1842, with a brief paragraph in German. See also Matruchot, Rev. Gen. Bot. **7:** 321, Pl. 16. 1895; and Bainier, Bul. Soc. Mycol. France **23:** 111–112, Pl. XV. 1907.

The essential characters given by Corda were: Conidiophores erect septate, penicillately branching above; branches and branchlets septate, appressed, forming a solitary gelatinous head; conidia unicellular, borne upon the tips of branchlets and held together by mucilaginous substance in a dense mass. The genus *Gliocladium* was thus described as reproducing the growth habits, mycelium, conidiophores and conidial apparatus of *Penicillium* except that the conidia borne successively from the tips of sterigmata did not adhere in chains but became enveloped in mucilaginous drops which increased in size with the increased numbers of conidia, followed by the fusion of the masses upon adjacent sterigmata, then often the fusion of these mucilaginous masses with those from adjacent penicilli to produce large balls of conidia. See figs. 168 and 169 of this Manual.

Matruchot (1895) described perithecia and ascospore formation in certain species but this has not been confirmed by others. In our experience, the forms constantly encountered in culture are purely conidial. Additional comparative studies of structure in conidial, and if possible ascosporic forms are necessary before *Gliocladium* and *Penicillium* can be accurately placed with reference to each other among the Ascomycetes.

Gymnoascus Baranetzky, in Bot. Zeit. **30:** 158. 1872.

Diagnosis taken from Saccardo Syll. **8:** p. 823. 1889: Ascogenous masses clustered, small, asci obovate, 8-spored; more or less surrounded by masses of mycelium; sporidia ovoid, hyaline 1-celled. In Sylloge **11:** p. 437 (1895), Saccardo transferred *Penicillium luteum* Zukal to *Gymnoascus*. Cultures have been constantly encountered with ascogenous structures showing the morphology of *Gymnoascus* and conidial structures definitely penicillate. Other species, obviously closely related, produce perithecia with more or less definite walls. We have hesitated to assign species so obviously belonging together to *Gymnoascus* if they are without wall, and to *Penicillium* if they show perithecial walls.

Isaria Persoon, in "Disp.," pp. 41, 74. 1797.

Many years ago, Atkinson (1894) pointed out the occurrence of Penicillium-like fruits in cultures known to arise from species of *Isaria*. This was readily demonstrated from time to time when insects bearing coremia of the Isaria-type were brought in and cultures were made from their conidia. Studies of these forms revealed a fairly characteristic type of structure. Occasionally one of these forms produces coremia in agar

suggestive of the insect parasite. Forms definitely recognizable as *Isaria* are not included in this Manual.

Lysipenicillium Brefeld, in Unters. Gesammtgeb. der Myk. **14:** 209–210. 1908; and **15:** Taf. VII, figs. 1–7. 1912. Type species: *L. insigne*; this was probably *Penicillium insigne* Winter, but identity is not claimed.

Brefeld, in describing *Lysipenicillium insigne*, separates a species which is shown by his descriptions and figures to represent a *Gliocladium*. He failed to give an adequate generic characterization, thus throwing upon one who chooses to accept the name the necessity of seeking the proper characterization in previous publications, none of which are cited. Thaxter (1922) expressed the belief that *L. insigne* of Brefeld was *Gliocladium penicilloides* Corda.

Metarrhizium Sorokin, in Zeit. der Kaiserlichen Landwirtschaflich Gesellschaft für Neurussland, Odessa **1879:** 268 (fide Pope, 1944). Type species: *Metarrhizium anisopliae* (Metsch.) Sorokin.

Synonym: *Entomophthora anisopliae* Metschnikoff, *ibid.* **1879:** 21–50. Vuillemin (in Bul. Soc. Mycol. France **22:** 214–222; Pl. 11, figs. 1–8. 1904) transferred the above species, which typically represents an insect parasite, to *Penicillium* as *Penicillium anisopliae* (Metsch.).

Metarrhizium is introduced here because species and strains normally produce conidial masses, or sporodochia, which superficially may suggest some coremiform *Penicillium* of the general aspect of *P. claviforme* Bainier. Whereas penicillate structures can be identified in these forms, careful examination of sterigmatic cells and conidia serves to differentiate between the much-branched and interwoven conidial elements of *Metarrhizium* (which typically form a hymenium-like palisade) and the generally separate and distinct fruiting structures of even the most strongly fasciculate *Penicillium*.

Pope (1944) described *Metarrhizium glutinosum* as a new saprophytic species with marked cellulolytic ability. Thom (1930, p. 434) had called attention to similar forms, without name, as common in soil and on decaying vegetation. White and Downing (1947) referred Pope's species to synonymy under *Myrothecium verrucaria* (Alb. and Schw.). Dimt. ex. Fr. Whether correctly designated as *Myrothecium* or *Metarrhizium*, these forms in laboratory culture may bear a striking resemblance to species of *Penicillium* or *Gliocladium* hence will pass through the hands of the user of this Manual.

Microaspergillus Wehmer, in Monograph. 1901.

Biourge included in his Monograph, under species names as *Penicillium*, a number of organisms figured with monoverticillate penicilli, which, when he finally sent them to us in 1928, had been relabeled as species of *Microaspergillus*. In every case examined, these species had the typical "foot-cell" of the Aspergilli (see Thom and Raper, p. 17. 1945) which in no case appeared in his previous drawings. On this basis alone, these organisms could be removed from *Penicillium*. The species under consideration are really Aspergilli belonging to the *A. restrictus* series of the *Aspergillus glaucus* group (see Thom and Raper, 1945). They are reported in this Manual only in the Species Index. Biourge took up the name *Microaspergillus*, previously introduced by Wehmer (1901), and made it include a series of very small and delicate forms mostly with a single series of sterigmata.

Monilia Persoon, emend. Sacc. in Mich. II, p. 17 nec Fr., in Sylloge IV, p. 31. 1886.

Saccardo's diagnosis translated: hyphae erect, widely branching; colonies fairly compact, rarely loose and spreading, bearing sporophores; conidia rather large in chains.

This genus has been insufficiently studied and is unsatisfactorily separated from *Oöspora*. Essentially Persoon included in his idea of *Monilia* any species with spores borne in chains, as shown by the forms assigned to the genus. Detailed figures or descriptions of the formation of such conidial chains were entirely omitted. *Penicillium* was included along with *Aspergillus* and many other forms. So far as its relation to *Penicillium* is concerned, Persoon's genus contributed nothing.

Monoverticillium Biourge, in Bul. Ass. Anc. El. Ec. Brass. Univ. Louvain, No. 3. 1920.

In his Monograph (1923) Biourge used Dierckx's name *Aspergilloides* on p. 31 to cover forms with simple verticils of sterigmata, but on p. 265 placed his own (1920) designation *Monoverticillium* (as a sub-genus) first and followed it with *Aspergilloides*.

Paecilomyces Bainier, in Bul. Soc. Mycol. France **23:** 26–27, Pl. VII. 1907. Type species: *Paecilomyces varioti* Bainier.

Synonyms: *Penicillium divaricatum* Thom, *Eidamia catenulata* Horne and Williamson.

Probable synonyms: *Corrollium* Sopp and some species of *Spicaria* Harz.

This genus was described as related to *Penicillium* and *Aspergillus*, and distinguished from them by its sterigmata which are short tubular or

more or less enlarged, tapering into long conidium-producing tubes mostly curved or bent slightly from the axis of the sterigmata; sterigmata occur variously in terminal groups approximating the appearance of a *Penicillium,* or partly in Penicillium-like verticils with conidium-bearing tubes and conidial chains divergent, partly variously arranged on short branchlets, or again occurring singly and laterally upon fertile hyphae; conidia elliptical; conidial areas *never* green. See fig. 170 of this Manual.

Bainier failed to describe accessory structures which appear more or less commonly in all strains, and very abundantly in certain members of this genus. These were regarded as macrospores by Horne and Williamson (1923) and made the basis of transferring these species to *Eidamia.*

Olliver and Smith (1933) described as *Byssochlamys fulva* an ascosporic form with a Paecilomyces-like conidial stage (see p. 951).

Scopulariopsis Bainier, in Bul. Soc. Mycol. France **23:** 98–104, Pl. XI. 1907. Type species: *Penicillium brevicaule* Saccardo.

Synonym: *Acaulium* Sopp, *q.v.*

Bainier's discursive description presented valid observations together with characters that seem to us untenable. Nevertheless, study of a great many strains of the group lead to the conclusion that these organisms are not closely related to the usual types of Penicillia, hence may properly be segregated. Since *Scopulariopsis* was published in 1907 and *Acaulium* Sopp in 1912, the former should be accepted. See fig. 171 of this Manual.

Scopulariopsis Bainier, was emended by Thom in The Penicillia, p. 28, 1930 as follows: Colonies never green; conidial apparatus partly Penicillium-like, partly in reduced and variant aggregations of sterigmata and branches or even single scattered sterigmata; sterigmata either Penicillium-like or more or less specialized, tapering gradually from a basal tubular section toward a conidium producing apex from which successive conidia are cut off by cross-walls. Conidia initially more or less pointed at the apex and truncate at the base with a more or less thickened basal ring surrounding a basal germinal pore, with walls usually thickened and often variously marked or roughened. Members of the genus appear as agents of decomposition after the usual green Penicillia have ceased to be active; that is, in the last phases of decay.

Emmons and Dodge (1931) described as *Microascus trigonosporus* a form with black ostiolate perithecia and the conidial phase of a *Scopulariopsis.*

Spicaria Harz, in Bul. de la Soc. Imp. des Naturalistes de Moscou **44:** 51. 1871.

Molds simulating Penicillia in appearance but bearing conidia on long tapered sterigmata that are borne in verticils and strongly divergent

are commonly assigned to the genus *Spicaria*. Conidial structures are typically freely branched, often in whorls, and may present the general aspect of a *Verticillium*. Relationship to *Penicillium lilacinum* Thom through forms such as *Spicaria violacea* Abbott is strongly suggested. Gilman and Abbott (1927) assigned to *Spicaria* the whole series which we would put in *Paecilomyces*.

Stysanus, in Sopp Monogr., pp. 78–79, 1912, is designated as a subgenus of *Penicillium*. Biourge (1923) follows Sopp in considering these forms to be related.

The species studied by Sopp produced Penicillium-like conidiophores, sterigmata, and conidia. He, therefore, argued that the fact that the separate conidiophores diverged from a column of hyphae, or for a part of their course formed such a column, did not warrant separation from the genus *Penicillium* any more than the coremia produced by *Penicillium glaucum* (*P. expansum*) upon apples warrants its exclusion from *Penicillium*. Sopp especially noted similarities of *Acaulium fulvum* and *A. violaceum* to *Stysanus stemonitis* and predicted that *Stysanus* as a genus would eventually disappear in *Penicillium*.

In our culture experience, species of *Stysanus* have dark to almost black cell walls and differ so markedly in general aspect as to suggest relationships widely divergent from *Penicillium*. Nevertheless, dematiaceous species occasionally appear with walls colorless in laboratory media during the first few days of growth. Thus, it is entirely possible that such species might be erroneously included among the Penicillia unless the observations are carried farther than we sometimes do. In older cultures significant differences are unmistakable.

Synpenicillium Costantin, in Bul. Soc. Mycol. France **4:** 62–68, Pl. XIV, figs. 10–17. 1888. Type species: *Synpenicillium album* Costantin.

Synonyms: *P. costantini* Bainier, Bul. Soc. Myc. France **22:** Pl. XI, figs. 1–6. 1906.

Coremium album (Cost.) Sacc. and Trav. Change of name only in Syll. Fung. **19:** 428. 1910; diagnosis Syll. **22:** 1444. 1913. Incorrectly spelled: *Sympenicillium* in Biourge's Monogr., p. 216. 1923.

Constantin created his genus *Synpenicillium* for one species, *S. album*, specifying as the generic characters the production of short conidiophores from fasciated (ropy) hyphae, and of aggregates of several conidiophores arising together from fasciated hyphae.

Bainier, regarding his species as identical with Costantin's, discarded the generic name and, since *Penicillium album* was preoccupied, proposed

the name *P. costantini* for this form. The name was again changed by Saccardo in the Sylloge to *Coremium*, but on inadequate grounds. Thom (1930, pp. 528–529) recognized Bainier's usage but followed Dale (1914) in placing the species in *Scopulariopsis*.

Chapter III

OBSERVATION AND DESCRIPTION OF PENICILLIA

A colony of *Penicillium* typically exhibits certain striking characteristics. These include color and color changes; texture which may be velvety, floccose, funiculose, or fasciculate or coremiform; and habit, which may be restricted to broadly spreading and range from plane to deeply furrowed or wrinkled. The substratum may or may not be discolored. Conspicuous drops of transpired fluid are characteristic of some species but not of others. Odors may or may not be produced, and if present may be fairly characteristic or just "moldy." Occasional records of changes in the color and appearance of the colony, and its effect upon the substratum, over a period of several weeks often provide useful information.

After a preliminary examination with the naked eye, the hand lens, and direct examination with the low powers of a compound microscope to establish cultural characteristics, a microscopic mount enables one to determine the details of structure and the pattern and dimensions of essential cells. Microscopic observations on *Penicillium* should begin within a few days and follow the development of the colony throughout the growing period, usually comprising the first two weeks, and should include examination of the submerged and aerial hyphae, the conidiophores, and the arrangement of the cellular elements which comprise the conidial apparatus.

Equipment

A good hand lens or low power binocular is extremely useful for making preliminary observations of colony characteristics. For closer examination, study of the fungus in petri dish cultures with the low powers of the compound microscope is essential to an accurate description of the colony itself. For making the necessary detailed studies of the penicillus apochromatic objectives are recommended, including if possible 16 mm., 8 mm., 4 mm., and either a 2 or 3 mm. oil immersion lens of 1.30 N.A. For use with these lenses one should have 10X and 15X compensating oculars, one of which is equipped with an eyepiece micrometer disk to afford constant provision for measurement of cellular elements.

Slide Mounts

Preparations for microscopic examination present many difficulties since the aerial parts of many Penicillia do not mix readily with water.

Hence, it is necessary to treat the preparation with a solvent such as ethyl alcohol prior to the addition of water or some mounting fluid. Water is satisfactory if observations can be completed within a few minutes. If the preparation is to be retained for several hours or even days for comparative examination with other specimens, some type of non-drying mounting fluid must be used. Weak glycerine (10–20%), with or without the addition of a stain such as eosin, can be used over a considerable period; and if allowed to concentrate, can be sealed to form a semi-permanent preparation. It has become routine practice in our Laboratory to wash preparations quickly in 70% alcohol and then mount in a fluid such as Amman's mounting fluid which neither plasmolyzes, swells, nor discolors the cells of most Penicillia. The composition of this mounting fluid, which was developed about 1896, is as follows:

Carbolic acid crystals (c.p.)	20.0 gms.
Lactic acid (sp. gr. 1.2)	20.0 gms.
Glycerine (sp. gr. 1.25)	40.0 gms.
Distilled water	20.0 ml.

The carbolic acid crystals are first liquefied by heating in a water bath.

Cultural Characteristics

color of conidial areas

Every description of a *Penicillium* emphasizes some color, or series of colors, as characteristic of conidial areas. If the describer uses several culture media, it is usually necessary to specify the color upon each by name or numerical reference in some of the recognized color standards. Our own records over a period of many years, including the current study, are based upon Ridgway's "Color Standards and Nomenclature" published in 1912. Much of the European literature is based upon Klincksieck and Valette's "Code des Couleurs" published in 1901. As yet no one has adopted the newer color manuals such as the "Munsell Book of Color" in which a greater number of hues and values are available for citation. Reference to such manuals will undoubtedly become necessary in the future since both Ridgway's and Klincksieck and Valette's works are out of print and no longer generally available. Illman and Hamly (1948), at the University of Toronto, are currently establishing the identity of Ridgway's color chips with specific color notations in Munsell's atlas.

Our records show considerable variation in color for particular strains as interpreted by different individuals, or by the same individual working at different times. For this reason, citation of color is never an absolute guide even though a particular shade is designated. In general, however, the colors produced by a given strain of *Penicillium* upon a standardized

substratum, grown at a definite temperature, fall fairly consistently within a narrow range of tints and shades of some particular mixture of colors, as for example yellow and green, blue and green, red and orange, orange and yellow, etc. The culture medium used, however, must be the first item specified if the color ranges which are cited are to have real value.

The range of colony colors within the genus *Penicillium* is quite wide. Included are a few forms that are white and others which show mixtures of orange and yellow with admixtures of red. The great majority of forms, however, develop colors in yellow-greens, greens, and blue-greens during their fruiting periods, thus accounting for the common lay reference to them as "green mold" or "blue mold." Many of these Penicillia lose all of their green color in age and assume various shades of yellowish brown, reddish brown, olive gray to almost fuscous. In none of the typical Penicillia, however, are the above colors accompanied by the heavy, brown cell walls characteristic of the Dematiaceae.

COLOR IN THE MYCELIUM AND SUBSTRATUM

The aerial mycelium in *Penicillium* is nearly always colorless. Areas of yellow and red hyphae commonly appear in the Biverticillata-Symmetrica section, and occasionally elsewhere, but when subjected to microscopic examination the coloring substance is found to be largely deposited as granules on the surface of the cell wall rather than within the cell itself.

The submerged mycelium of various species and groups, on the other hand, shows a series of yellow, orange, red, brown, lilac, or hyacinth colors with occasional green and even black areas appearing. Such colors are best seen from below and are routinely designated as color of reverse, or simply "reverse."

Pigment production in the mycelium, even more than in conidial areas, is influenced by changing the nutrient composition of the substratum. Hence, it is always essential to specify the character and composition of the substrate employed when citing any color as characteristic of the mycelium of a particular strain, species, or series.

Whereas contrasts in color may occur in some series, in the majority of cases certain *ranges* of color are found to be correlated with fairly consistent morphological characteristics. Within a given series a particular species may be able to carry color production up to a certain point represented by an identifiable tint or shade. Another related species, beginning at the same point, may carry the process further, and a third species may carry it still further. This is well illustrated in the *Penicillium purpurogenum* series.

The coloring matter present in the submerged mycelium may or may not

diffuse into the substratum. In some species the substratum is quickly discolored and follows the color changes of the mycelium. In other species the color is retained within the hyphal cells. Such contrasting conditions may occasionally occur in species believed to be closely related. For this reason, differences in color are often believed to reflect minor changes in biochemical reactions rather than differences of fundamental importance.

The part played by oxidation in successive color changes has not been worked out systematically but is indicated by isolated observations. For example, in cutting open a fresh Roquefort cheese containing a pure culture of *Penicillium roqueforti* the mold is sometimes first seen as yellow but changes to deep green within a very few minutes after being exposed to air.

Within recent years Raistrick and others have initiated a study of the pigments produced by the Penicillia which may in time help to clarify relationships within this genus. Several of the pigments described act as indicators, changing color when the reaction is shifted from acid to alkaline and *vice versa*.

APPEARANCE AND TEXTURE OF COLONIES

By examination with the naked eye, the hand-lens, and the low powers of the compound microscope, it is possible to establish four fairly well-defined colony types, namely: velvety, floccose or lanose, funiculose, and fasciculate or coremiform.

Velvety (fig. 3A): Colonies are regarded as velvety or velutinous if all, or nearly all, of the vegetative hyphae are submerged in the nutrient substratum, and if the conidiophores rise above the surface in a fairly dense and even stand. Such colonies give the appearance of a surface of velvet, or of a field of grain in miniature. Colonies of this type are characteristically produced in such species as *Penicillium frequentans* Westling, *P. oxalicum* Thom, *P. roqueforti* Thom, and *P. chrysogenum* Thom (fig. 3A). Velvety colonies are, as a rule, comparatively thin but may, upon occasion, range up to 0.5 to 1.0 mm. or more in depth.

Floccose or lanose (fig. 3B): Other species, for example *Penicillium camemberti* Thom and *P. caseicolum* Bainier (fig. 3B) produce a cottony mass of branching and interlacing hyphae evenly or unevenly over the surface of the nutrient medium. At a characteristic period in their development, conidiophores appear as branches of these aerial hyphae. Conidial areas usually appear first in the center of the colony and gradually extend toward the margin. Throughout the growing period a sterile white, or in some cases yellowish, margin surrounds the fruiting area, but

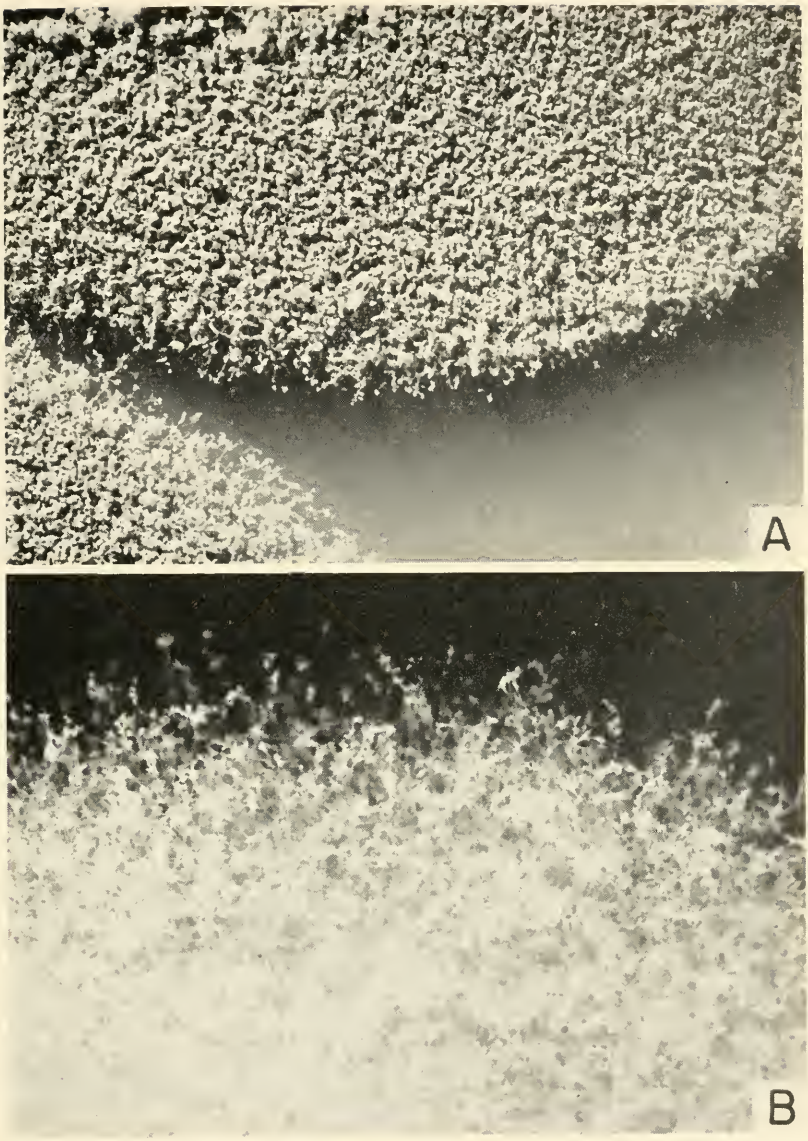


FIG. 3. Types of colony surface and margin. *A*, *Penicillium chrysogenum* Thom, marginal area of a typical *velvety* colony, × 9.0. *B*, *P. caseicolum* Bainier, marginal area of a typical *lanose* colony, × 20.

when growth ceases the fruiting area commonly extends to the very edge of the colony with conidiophores commonly arising from the substratum.

Velvety and floccose colonies are sharply differentiated in their extreme

forms. In the actual study of large numbers of cultures, however, every gradation between these extremes is found and it often becomes a matter of the judgment of the observer as to the group to which the strain under observation should be assigned. For descriptive purposes, colonies which show a definite and fairly deep aerial felt before the beginning of conidium formation are regarded as lanose or floccose; colonies in which conidial areas follow closely the growth of the mycelium at the colony margin, and do not develop an aerial felt, are regarded as velvety. Modified terms, such as "deeply velvety," have to be introduced occasionally.

Funiculose (fig. 4A): Some species are characterized by aerial ropes, bundles, or funicles consisting of several to many hyphae. Such bundles may be ascending (fig. 4A) but are rarely, if ever, upright. In the so-called funiculose species, part or all of the fertile hyphae arise as branches from these ropy networks, although simple conidiophores are also found. The funiculose type of colony may be found in each of the major sections of the genus *Penicillium*, and also in the "related" genera *Scopulariopsis* and *Paecilomyces*.

Funiculose masses of aerial hyphae are readily determinable with the lower magnifications of the compound microscope and afford a useful character in the grouping of species. The character is seized upon simply as a useful diagnostic tool rather than an indication of natural relationship since no genetic significance seems to be attributable to its development. Caution should be exercised in interpreting ropiness as a final diagnostic characteristic, because strains from non-funiculose series often tend to develop ropes of aerial hyphae when they become "wet" or otherwise atypical in appearance. If the character is applied, however, to cultures freshly isolated from nature, or to those long maintained in the laboratory without apparent change, it can be extremely useful.

Fasciculate or Coremiform (fig. 4B): A whole series of forms show the marginal areas of rapidly growing colonies to be rough or granular, or "mealy," to use Westling's designation. Microscopic examination in such cases shows that the rough or mealy appearance is due to the aggregation or fasciculation of conidiophores. In some species, fascicles may be at first clearly noticeable in marginal colony areas, only to become largely obscured later by the crowded development of simple conidiophores in the intervening spaces. In a few cases, such as *Penicillium italicum* Wehmer, the coremiform structures characteristically appear late in colony development. In other species, such as *P. granulatum* Bainier (fig. 4B), the vast majority of the conidiophores are from the first aggregated into well-defined fascicles. Occasionally, in species such as *P. claviforme* Bainier, conidiophores develop almost exclusively in compact columns, or "stalks", which produce single integrated conidium-bearing heads (fig. 140B).

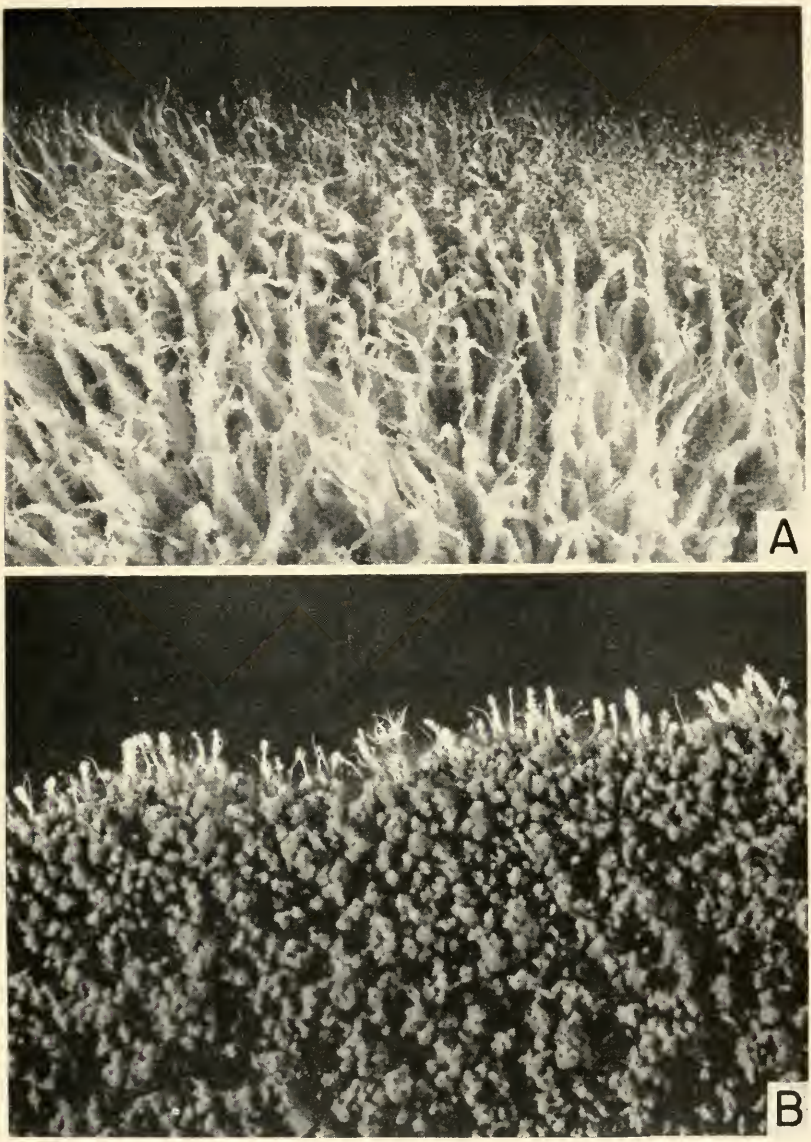


FIG. 4. Types of colony surface and margin. *A*, *Penicillium pallidum* Smith, marginal area of a strongly funiculose colony, × 8.5. *B*, *P. granulatum* Bainier, marginal area of a strongly *fasciculate* colony, × 8.5.

Types in which simple conidiophores do not often appear have been commonly described in the literature under such generic names as *Coremium*, *Stysanus*, *Isaria*, etc. (see Chapter II).

Various authors have discussed the phenomenon of coremium formation in *Penicillium* and related genera (Wächter, 1910; Blochwitz, 1925; and others). Some investigators hold that coremium formation may be induced in any *Penicillium* by proper culture methods, while others maintain that coremium formation is an inherent characteristic of certain species only, and becomes evident whenever certain favorable conditions prevail. Our own observations indicate that coremia may arise in connection with two forms of antecedent structure: (1) the development in the mycelium of trailing or ascending ropes of hyphae, or (2) the development of all or part of the conidiophores into clusters or fasicles. An accentuation of either tendency leads directly to structures described as coremia.

When grown in laboratory culture a few species, such as *Penicillium claviforme*, retain a strictly coremiform habit. Other species, including *P. expansum* Link, normally produce conspicuous coremia in their natural habitats, but tend to lose this characteristic when grown on the usual substrata of the laboratory.

COLONY MARGIN

Correct information concerning the relation between submerged mycelium, aerial hyphae, and conidiophore origin can be best established at the margin of the growing colony. The period of satisfactory observation begins after three or four days in rapidly growing species and ends as a rule with the cessation of growth during the second week. For slower growing species the period for critical observation necessarily begins later and lasts longer. In some species the mass of mycelium is sufficiently dense and the growth sufficiently abrupt to interfere with satisfactory use of the compound microscope at the colony margin. Usually, however, by selecting petri dishes in which two or more colonies are present, essential observations can be made in the inter-colony area where the rate of growth is reduced and where the process of fruiting is accelerated. It is primarily with this end in mind that our cultures are usually planted with three colonies to the culture plate.

COLONY GROWTH

At the initiation of colony growth the germ tubes quickly elongate, divide into cells by septation and branch extensively to form closely woven networks or felts of mycelia. In a favorable nutrient evenly distributed as in a petri dish the resulting colonies are usually approximately circular, although marginal areas may be characteristically even, notched or stellate, or crenulate because of the establishment of main radiating hyphae from

which the interspaces are filled by branching systems. Muller (1922), working with a strain reported as *Penicillium glaucum*, attributed this radial habit of growth to negative chemotropism toward its own metabolic products which accumulate most rapidly toward the center of the colony. Smith (1923), working with a strain of *P. expansum*, reported that growth in length occurred only at the tips of the hyphae. Cells once formed might throw out branches with new growing points but the cells themselves did not increase in length during the period of observation. Such a theory might account for the plane surfaces of *P. expansum* or *P. roqueforti*. It cannot, however, account for the contorted, cerebriform or radiately wrinkled mycelia of such species as *P. stoloniferum* on Czapek where the progressive folding of the colony must result from a continuing lateral growth of mycelial elements.

ZONATION

Surface growth in zones is a conspicuous feature in many species and was discussed extensively by Munk as early as 1912. Biourge, in his subgenus *Eupenicillium*, made zonation the diagnostic character of one Subsection and assigned to his hemizonate series of that Sub-section forms which were indistinctly or indefinitely zonate. It has seemed to us, from an examination of Biourge's descriptions and his cultures, that this basis of grouping throws together too many forms of divergent relationship. Zonation (fig. 5), often very conspicuous and sometimes fairly constant for certain species, is an unanalyzed growth habit occurring in different series throughout the whole genus. It may better be linked with other characters than used as a primary basis for taxonomic separation. Zone production in some species is only transiently evident in the early stages of colony growth; again it appears only at the latter end of growth and in inconspicuous degrees. Some species are zonate when grown upon one substratum and not upon other substrata. It has seemed best, therefore, to disregard Biourge's major groupings based upon zonation and to use this character only in the separation of members in series held together by more fundamental characters.

Ullscheck (1928), following somewhat the arguments of Munk (1912a), offered the hypothesis that zones appear when colonies grow rapidly, secrete enzymes and by-products of their metabolism in sufficient concentration to reduce or suppress growth and fruit formation in those bands. The mycelium then advances into fresh nutrients, resumes vigorous growth and produces an abundance of fruit, only to be depressed again by the excessive by-products of this heightened activity. The extension of such a colony gives the appearance of zonation.

EXUDATE

Transpiration of fluid is a conspicuous feature of some growing colonies, evident but inconspicuous in others, and wholly lacking in still others. Where transpired fluid, or exudate, accumulates in drops it becomes a conspicuous feature of the growing colony, usually marked by a fairly constant color for a particular species. Sometimes the production of

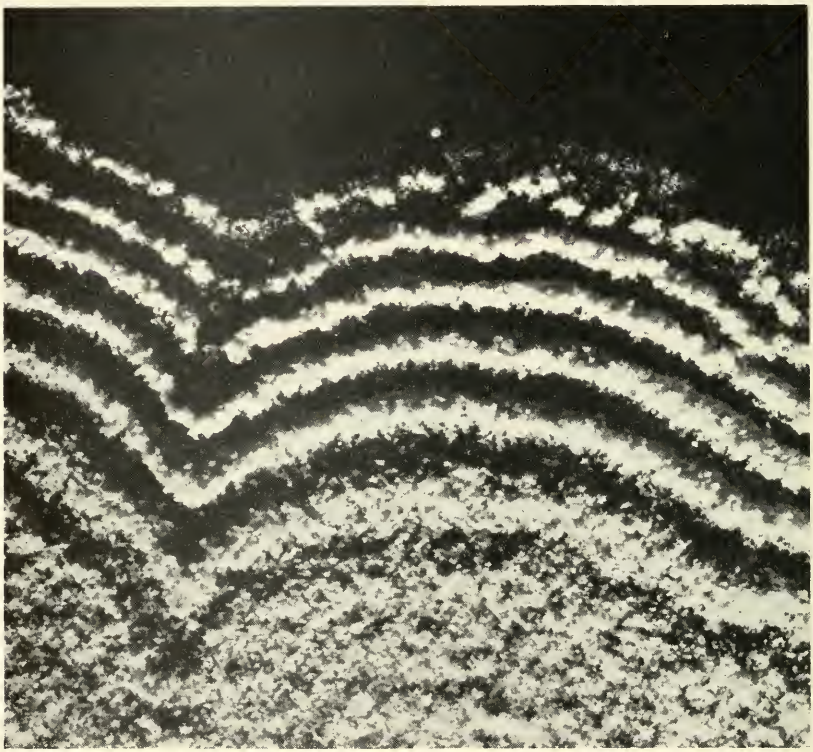


FIG. 5. Conspicuously zonate colony developed by a white-spored mutant of *Penicillium urticae* Bainier, × 18.

exudate of a general color is characteristic of an entire series, as for example in the formation of yellow exudate by members of the *Penicillium chrysogenum* series (fig. 6). In such a case it aids materially in establishing broad relationships.

Evaporation in older colonies frequently leaves residues upon the surface of the conidial area, and may create depressions where conidial masses were pressed down or held aside by the weight or mass of the transpired fluid. These residues and drops must be correctly interpreted else they

may be quite misleading. Biourge, for example, proposed the name *P. pezizoides* for a member of the Fasciculata approximating *P. puberulum* Bainier in which the droplets upon evaporation left conspicuous pezizalike craters, pink in color. Another disturbing factor introduced by these drops is the not infrequent germination of conidia followed by secondary growth in the transpired fluid. When this occurs it often results in the formation of globose mycelial masses upon the surface of the colony which may erroneously be interpreted as fasciculate in origin and structure.

ODOR

Characteristic pungent or penetrating odors are produced by many species of *Penicillium*. Usually these are referred to as "moldy" or

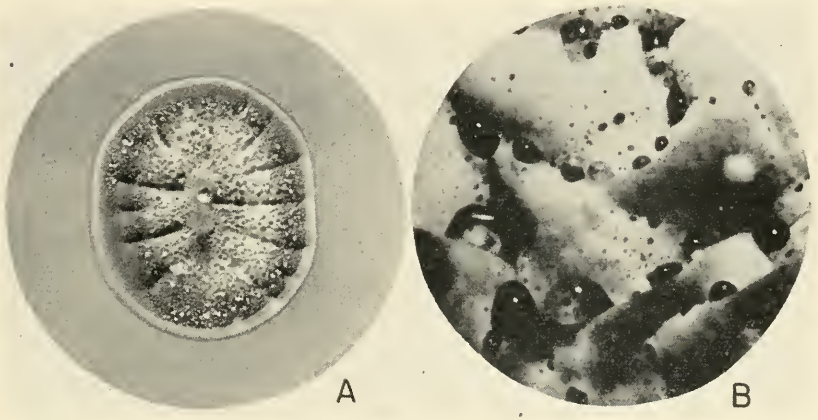


FIG. 6. Exudate formation in *Penicillium notatum* Westling. *A*, Colony showing abundant exudate, or drops, × 2. *B*, Enlarged area of the same, × 15.

"musty," but such nomenclature is very unsatisfactory due to the varying response of different individuals when confronted with the same preparation. Due to this variability, one is often unable to interpret terms previously used or to insure an understanding of the terms being proposed. Odors have some apparent taxonomic significance in a limited number of cases. Among the Fasciculata, wherever odors are produced, these are usually diagnosed as "moldy" and vary from slight to very intense in certain cases such as *Penicillium claviforme* and *P. olivino-viride*. Among the biverticillately symmetrical forms, species assignable to the *P. purpurogenum* series are usually characterized by a fragrant apple, or in age a walnut-like, odor which is particularly marked upon malt agar. *Penicillium digitatum* in laboratory culture produces a characteristic odor variously described as that of spoiling citrus fruit or unpickled dill,

Penicillium decumbens regularly produces a perfume-like odor suggesting castile soap. Suffice it to say that in a limited number of cases odors are sufficiently distinctive to indicate presumptive relationships, but in the great majority of cases they afford unreliable and questionably useful criteria for species identification or separation.

Variations and Mutations

The Penicillia represent an unusually variable group of molds, and although successful taxonomy and nomenclature must be based upon strains considered to be "normal," the worker must recognize that variations and mutations often occur. In laboratory cultures, these usually arise in one of two ways. They may develop as a result of progressive change under continued laboratory cultivation and appear as sectors or areas of altered coloration, colony texture, or rate and habit of growth (Col. Pl. I). On the other hand, they may appear as limited sectors or areas showing an abrupt change in some conspicuous character such as color of ripe conidia or an inability to develop normal conidial structures upon the substratum employed. The latter type of change commonly remains stable through subsequent recultivations, hence may be regarded as a true mutation; the former type often continues to show further change in the same, or in some other direction, hence is usually regarded as representing a sort of step in a process of progressive variation. Strains believed to represent both types of development may be isolated from natural sources.

If reasons exist for believing them to represent merely different aspects assumed by a common and cosmopolitan species such variations or mutations are usually not accorded taxonomic status. For example, in the species *Penicillium citrinum* Thom, some strains show marked differences in colony texture and in the amount of sporulation under the usual conditions of culture. Another strain produces conidia that are tan to avellaneous in color. Still another fails to utilize nitrate nitrogen. None of these are, however, regarded as warranting specific or varietal status since they apparently conform with *P. citrinum* in every other way, and since variant or mutant strains have been artificially produced in other species which differ from the normal parents in seemingly identical ways.

Color Mutations

Mutations based upon the color of mature conidia are among the most common and the most conspicuous types encountered. As a rule these are either white (i.e., completely colorless) or show some tan to avellaneous shade. White mutants have been isolated from *Penicillium chrysogenum*, *P. notatum*, *P. urticae* (Col. Pl. I), and a strain formerly considered as *P. sartoryi* Thom but now regarded as a variant of *P. citrinum*. Tan

PLATE I

Natural mutations in species of *Penicillium*

TOP: Penicillium notatum Westling, showing the normal parent strain, NRRL 832 (dark blue-green colony), and a mutant, NRRL 832.A26, marked by the production of an abundant pink aerial mycelium. Steep agar; 12 days. *BOTTOM: Penicillium urticae* Bainier, showing the normal parent strain, NRRL 2159 (light blue-green colony), and a mutant, NRRL 2159.A, characterized by colorless conidia. Czapek's solution agar; 12 days. (Color photographs by Haines, Northern Regional Research Laboratory. Reproduced through co-operation of Chas. Pfizer & Co., Inc.)

mutants are known for *P. frequentans*, *P. notatum*, *P. chrysogenum*, and *P. rugulosum*. In none of these cases do the mutants seem to differ, except in conidial color, from the parent strains as these are maintained in culture, hence they are not regarded as separate taxonomic entities. Thom, in 1930, established *P. digitatum* var. *californicum* to identify a white conidial form, obviously representing *P. digitatum* in morphology and physiology, which was sent to him by Professor Fawcett in California. Recognition of this variety should probably be withdrawn since it does not differ from the typical species more than any of the above color mutants differ from the normal "green" parent cultures from which they were derived. Color mutants similar to the above are regularly encountered among the strains developing from conidia exposed to artificial stimuli such as ultra-violet and X-ray radiation, neutron bombardment, etc. They have been reported by Raper and Fennell (1946), Beadle (correspondence), Hanson, *et al.* (1945), and others.

Not all white or tan-spored Penicillia can be regarded as mutants. *Penicillium caseicolum* Bainier, for example, is characterized by colorless conidia, yet has been recognized as a valid species significant in the ripening of soft cheeses of the Camembert type for more than four decades. More recently George Smith (1939) described a species, *P. carneo-lutescens*, which produces conidia light pink in color but is not known to closely approximate any recognized green-spored form.

DEFICIENCY MUTATIONS

Mutants characterized by striking nutritional deficiencies are sometimes isolated from nature, and regularly occur in considerable numbers among strains developing from conidia exposed to radiations or other external stimuli. In addition to the above mentioned strain of *Penicillium citrinum* which is unable to utilize nitrate nitrogen, we have also identified an isolate of *P. purpurogenum* which is unable to utilize sucrose due to an apparent invertase deficiency. Several additional strains have been observed to develop in a manner typical of well-recognized species upon an enriched medium such as steep agar, but to grow sparsely and very atypically upon standard Czapek's agar. In these latter cases nutritional deficiencies, unidentified as yet, obviously exist. To a considerable degree *P. tardum* behaves like a mold suffering from some type of nutritional deficiency (see pp. 651–653).

Working with *Penicillium notatum* and *P. chrysogenum*, Bonner (1946) reported the production of a whole series of mutations characterized by their inability to produce various essential vitamins and amino acids. Mutations of well-recognized species characterized by nutritional deficiencies, like those based upon color, are not accorded taxonomic status;

but recognition of their existence is essential to the establishment of a reliable nomenclature.

STERILE OVERGROWTHS

Areas of sterile, or essentially sterile, overgrowth may at times develop in otherwise typical strains of almost any species of *Penicillium*. Such overgrowths appear to be particularly characteristic of certain species, hence may introduce problems in identification and assignment. For example, *Penicillium solitum* Westling not uncommonly exhibits such developments in central colony areas after 10 to 14 days, and colonies of *P. italicum*, *P. cyclopium*, and other species often show developments of flocculent, non-sporulating mycelium which may materially alter the cultural aspect of strains unless special precautions are taken to eliminate such variant growth. In the case of *P. schneggii* Boas, the occurrence of sterile mycelial tufts was long recognized as a specific and diagnostic character; minimizing the significance of such tufts, we have in the present Manual assigned this species with *P. granulatum* Bainier with which species it is otherwise closely similar. Quite commonly, sterile overgrowths can be isolated and continued in separate culture where they exhibit little if any of the characteristics of the parent strains.

Miscellaneous Types

Whereas the above are among the types must commonly encountered, many other kinds of variants and mutants have been observed among the Penicillia. During the search for better penicillin producing molds, conducted at the Northern Regional Research Laboratory and elsewhere, variant strains showing the most diverse cultural characteristics were isolated and studied (fig. 30). It is outside the scope of the present Manual to discuss these in detail or to list the various types observed, but it is important that the student of the Penicillia should be cognizant of the range of variations which may be secured when a few selected strains are investigated intensively. For detailed discussions of variation, natural and induced, in members of the *Penicillium chrysogenum* series, the reader is referred to papers by Raper, Alexander, and Coghill (1944), Hansen and Snyder (1944), Pontecorvo and Gemmell (1944a and 1944b), Raper and Alexander (1945b), Hanson, *et al.* (1945), Sansome (1946), Raper and Fennell (1946), Whiffen and Savage (1947), Bonner (1947), and others. There is little doubt but that an equal range of variant types could be obtained from almost any species of *Penicillium* selected for equally intensive study.

Details of Structure

CONIDIOPHORES

Essential data regarding conidiophores include their length, septation, the diameter of their cells, and especially their origin in relation to the substratum and to each other. The walls of the conidiophores may be smooth and thin or may be variously roughened, with aerial portions appearing delicately echinulate, granular, or asperulate. In some cases, such as *Penicillium roqueforti*, these may be marked by conspicuous concretions or warts. Differences in the conidiophore wall run consistently through certain series of species, hence must be carefully observed. In other series this character tends to vary markedly with the culture medium. For example, in certain species of the Fasciculata and Divaricata, conidiophores may appear smooth upon Czapek but definitely rough upon malt agar. Separations of considerable usefulness, however, can still be based upon this character since species belonging to some series appear to be capable of developing roughness under all, or certain specific conditions; whereas the conidiophores of species belonging to other series remain smooth under all conditions.

Although extremes of variation in the length of conidiophores are usually marked in any culture, the majority of conidiophores in most cultures will approximate an average length. This length, to be most reliable, must be taken from the origin in another hyphae to the lowest branch of the penicillus. Valid data on conidiophore lengths in many species can be best obtained by direct observation of the undisturbed colony under the microscope instead of by the study of fluid mounts.

The conidiophore may be simple and unbranched, or variously branched. It may arise from vegetative hyphae within the substratum or from aerial vegetative hyphae variously arranged. It may stand alone, or be more or less closely aggregated into clusters, fascicles, or definite coremia.

The conidiophore of *Penicillium* typically lacks the differentiated foot-cell so characteristic of *Aspergillus* as indicated by Thom and Church in 1926 and subsequently by Thom and Raper (1945). While species with difficulty interpretable structures are sometimes found, the distinction remains generally definite and rather easily demonstrable. Exceptions are seen in George Smith's two species, *Penicillium varians* and *P. pallidum* (1933), where structures simulating, if not actually representing, foot-cells are regularly seen. In these cases, however, the patterns of conidial structure so complete aligns these forms with *Penicillium* as to leave no question regarding their proper assignment in this genus.

THE PENICILLUS

The penicillus (German: "pinsel") is understood to cover the whole branching system (fig. 7) and is measured from the lowest branch upon the main axis to the tips of the sterigmata, or conidium bearing cells. Conidial

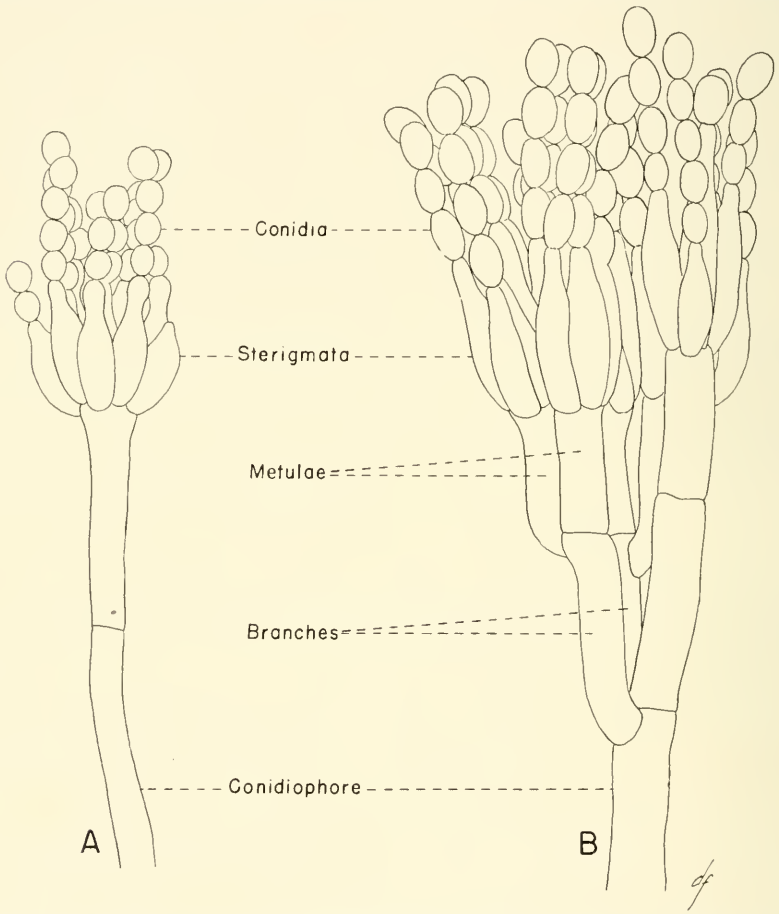


FIG. 7. The Penicillus. *A*, Typical monoverticillate penicillus, as seen in *Penicillium frequentans* Westling, consisting of a terminal verticil of sterigmata only. *B*, Typical asymmetric penicillus as seen in *P. expansum* Link, showing metulae and branches below the sterigmata. Camera lucida drawings, × 1600.

chains are excluded. For diagnostic purposes, the average dimension and the range of variation in the branching system must be determined, rather than the measurement and description of a few selected penicilli. The type of penicillus most common to the species can best be determined by studying preparations which make possible the rapid comparison of large num-

bers of fruiting structures. This can often be done most readily by direct examination of the colony in the petri dish. Habit sketches, made with the aid of a camera lucida, showing the relative size of penicilli, the types of branching observed, and the arrangement of the conidial chains can be very useful.

In describing species, or in the identification of unknown strains, the type of penicillus most commonly produced must be determined since allocations to major sections are made upon this basis.

Penicilli are regarded as monoverticillate if each terminal branchlet, with its cluster of sterigmata and conidial chains, seems to stand out separately (fig. 8). Such penicilli may be strictly monoverticillate, i.e., borne upon separate conidiophores which arise either from within the substratum or from trailing vegetative hyphae; or they may be ramigenous, i.e., borne as an irregular series of branches at various levels upon a common fertile hyphae. In some forms conidial structure seems to consist of terminal groups of monoverticillate heads, but these can best be assigned to another section, usually the Divaricata.

Penicilli are regarded as biverticillate if branching occurs at two or rarely more than three levels. Such penicilli may be either symmetrical or asymmetrical. If the two groups of branches are regularly and evenly spaced about the central axis, the penicillus is regarded as biverticillately symmetrical, and is characteristic of a major section of the genus, the Biverticillata-Symmetrica (fig. 10). If the penicillus appears to be asymmetrical, one-sided, or lop-sided, the strain or species belongs among the Asymmetrica, in which the branches are characteristically alternate, or form incomplete whorls about a central axis (fig. 9).

A few species have been described by Bainier (1906–1907) with penicilli several times verticillate below the level of the sterigmata. While these forms doubtfully represent true Penicillia, they are recognized as constituting a section, the Polyverticillata, since they are occasionally encountered and superficially at least, closely resemble *Penicillium* (see Chapter XIV).

In any case the description should indicate the arrangement of parts, the general pattern, and the number of series or levels in the branching system that appear to be most characteristic of the species or strain under observation. Many difficulties will be encountered, and of necessity much depends upon the experience and judgment of the individual worker. Reduced conidial structures can be found in every species and strain of *Penicillium*. Generally, however, such reduced penicilli are few in number in the non-monoverticillate sections. In describing the penicilli in any given strain or species it is almost axiomatic that one should observe and record the maximal pattern of penicillus development. Whereas

strains that are typically biverticillate often produce reduced conidial structures, strains that are typically monoverticillate seldom develop larger and more complex structures. Interpreted in this way, there is for every species a general type, number, arrangement, and size of elements which can be described in fairly tangible terms. Drawings and photo-

FIG. 8. Types of conidial structures, or penicilli. Typical monoverticillate penicilli as seen in *Penicillium purpurrescens* (Sopp) n. comb., × 1500.

micrographs show in detail the pattern and cellular structure that are regarded as characteristic of particular species or strains. The written description, however, should be broad enough to include the range of patterns and dimensions that occur. It is possible to make descriptions either too restrictive or too inclusive.

For purposes of discussion, our consideration of the elements in the penicillus will begin with the terminal cells (sterigmata) which bear the

conidia, since these are common throughout the group, and will progress backward toward the main conidiophore (fig. 7):

Sterigmata

The differentiated conidium-producing cell, characteristic of *Penicillium* and related genera, is variously named the sterigma (plural, sterig-

FIG. 9. Two types of conidial structures, or penicilli, seen in the Asymmetrica. *A*, Typical divaricate penicillus of *Penicillium nigricans* (Bain.) Thom, a member of the Divaricata sub-section. × 1200. *B*, A typical, compact penicillus of *P. stoloniferum* Thom, a member of Velutina sub-section. × 1200.

mata), conidiiferous cell, basidium, or following Vuillemin (1910) phialis (plural, phialides). Biourge adopted the latter usage as have G. W. Martin and many other mycologists in America. Since the term sterigma has been more widely accepted, it will be used here. The sterigma as it applies to the Penicillia, may be defined as a transformed and highly differentiated cell with a tubular body of fairly typical length and diameter that is characteristically narrowed to a conidium producing tube, or tip, from which unicellular conidia are cut off successively to form a chain of varying length, depending upon the species and the conditions of culture. The resulting chain is characterized by fully ripe cells at its distal

end and developing cells at its base, and may contain up to several hundred conidia.

The sterigma of most monoverticillate forms, and most of the Asymmetrica as well, is a cylindrical cell with an acute, more or less tapering apex forming a tube roughly half the diameter of the sterigma (fig. 11A).

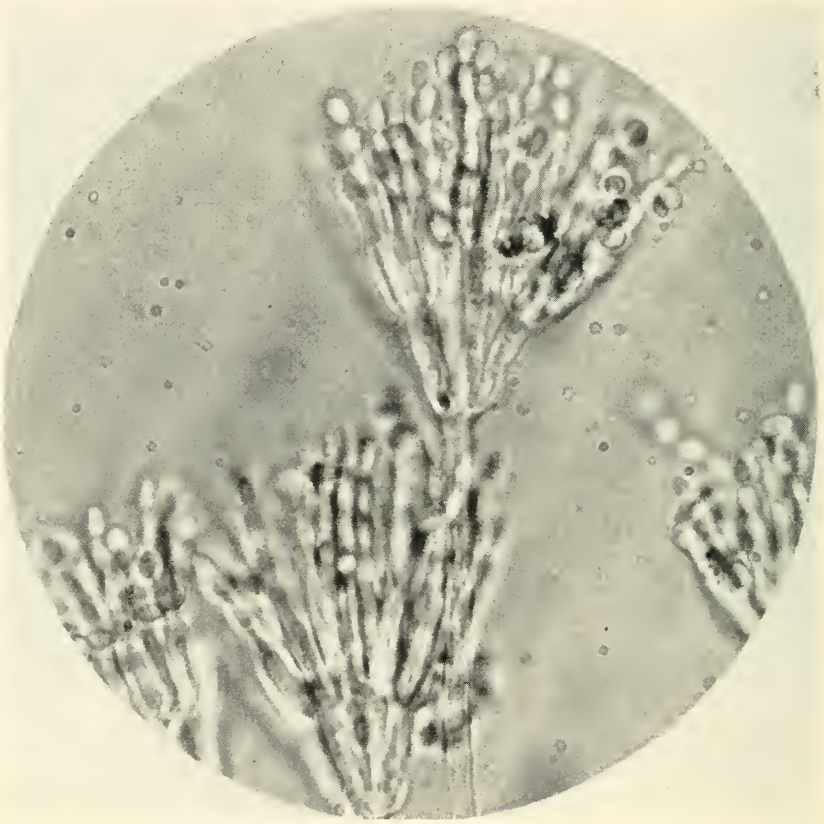


FIG. 10. Types of conidial structures, or penicilli. Typical biverticillately-symmetrical penicilli as seen in *Penicillium variabile* Sopp, × 1200.

In the *Penicillium janthinellum* series the sterigma tapers abruptly and produces a conspicuous terminal tube of fairly uniform diameter (fig. 11B). In the Biverticillata-Symmetrica the sterigma is generally smaller in diameter and longer and narrows more slowly (acuminately) at the apex to a smaller and evenly tapered tube—the mature cell being best described as lanceolate (fig. 11C). In *Paecilomyces*, a genus commonly regarded as closely related to *Penicillium*, the sterigma typically consists

of a short basal tube narrowed to a long neck which is characteristically bent from the main axis of the sterigma (fig. 11D).

The first sterigma in a verticil is a terminal cell which becomes transformed into a spore producing organ, the second pushes out from the cell below at the base of the first, and successive sterigmata bud out to form a whorl, verticil or cluster, on the apex of the main axis or some secondary branch thereof. The apex may be unchanged in size or variously enlarged toward the appearance and proportions of the vesicle of a small *Aspergillus*. The number of sterigmata in the verticil may be few and readily determinable, or sufficiently large to render determination entirely impractic-

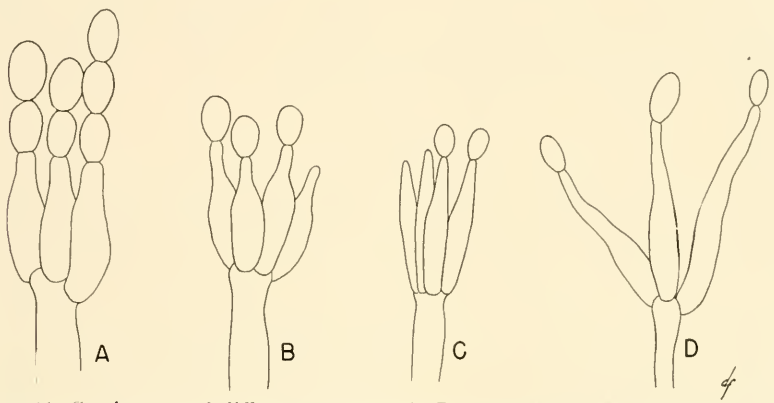


FIG. 11. Sterigmata of different types. *A*, *Penicillium expansum* Link, showing sterigmata of the type developed in most species of *Penicillium*. *B*, *P. janthinellum* Biourge, showing a type of sterigma with conspicuously narrowed conidium bearing tube that is characteristic of the *P. janthinellum* series and certain other species including ascosporic members of the Monoverticillata. *C*, *P. funiculosum* Thom, showing lanceolate sterigmata of the type characteristic of the Biverticillata-Symmetrica. *D*, *Paecilomyces varioti* Bainier, showing characteristic long-tapering sterigmata with tips often bent away from the main axes of the sterigmata. Camera lucida drawings, × 1500.

able. In any case, and contrary to the figures of some early workers, absolute regularity of parts is seldom if ever observed.

Metulae

The cells bearing the sterigmata in biverticillate forms are known as metulae (fig. 7B). These are characteristically borne in a terminal verticil on the main axis of the conidiophore, or on the main axis and one or more branches from it. If we accept the sterigma as the primary conidium-producing organ, the term metula may properly be restricted to apply to the characteristically differentiated members of the second series of branches, each supporting a group or verticil of sterigmata. They have

been variously termed branches, basidia, secondary sterigmata and finally metulae by Westling (1911).

The metulae usually follow closely the diameter of the conidiophore and whatever branches it may produce; less commonly they may be conspicuously smaller in diameter. They are often somewhat enlarged at the tip. In length they may vary quite appreciably or be more or less constant depending upon the species and strain. They generally average a little longer than the sterigmata and their arrangement is fairly characteristic of the species. Variations in shape are usually such as may be attributed to the effect of crowding several elongated cells into a compact verticil upon the apex of the fertile branch. Whenever the walls of the conidiophore are smooth, those of the metulae are also consistently smooth. When the walls of the conidiphore are pitted or rough, the walls of the metulae may or may not be similarly roughened.

Branches

In the larger penicilli produced by some of the Asymmetrica, where more than one verticil of metulae is developed, the cells, other than the main axis which bear such metulae, are referred to as branches (fig. 7B). In certain species the penicillus is usually typified by a single branch; in others one or more branches may be produced. However, in many forms, including the members of the Biverticillata-Symmetrica, branches are seldom if ever produced and the metulae are borne only as a terminal verticil on the main conidiophore axis. Biourge referred to branches as *rami*.

CONIDIA

Every conidium arises theoretically as a cylindrical body cut from the tube-like tip of a fertile cell, or sterigma. Changes from the cylindrical form may begin well before the separation of the cell has become evident by the formation of a definite cross-wall, or this may be delayed. In a few forms, such as *Penicillium digitatum* Saccardo (fig. 12A) and *P. italicum* Wehmer, the cylindrical shape of the conidia persists for a considerable time before it gradually becomes transformed to elliptical. In still other species, such as *P. bacillosporum* Swift, the conidia retain a cylindrical shape indefinitely (fig. 153). In the Biverticillata-Symmetrica the conidium typically first appears as a long cylindrical segment of small diameter, and tends to become fusiform by an increase in diameter at its center. In other species the length of the original segment is only a little greater than its diameter, hence the conidium quickly becomes globose or subglobose. In still other species it starts out as an elliptical segment and reaches a globose form by a general and continued swelling of the en-

tire developing cell. Although conidia in certain species have been described as globose at first, becoming elliptical in maturity, no evidence of this condition has been seen by us. The individual conidium usually attains the characteristic size, shape, and markings for a given species by the time a half dozen newer conidia have been cut off between it and the sterigma. Thereafter, walls may thicken somewhat and markings may become more accentuated, but otherwise little visible change occurs irrespective of the time the conidium may remain attached in the chain.

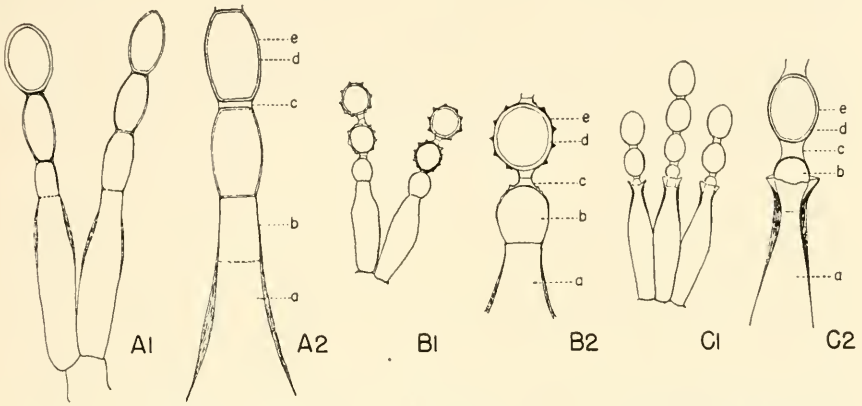


FIG. 12. Conidium formation in *Penicillium*. *A*, *P. digitatum* Saccardo: A_1, Camera lucida drawings of sterigmata and attached conidia; A_2, Diagrammatic representation of conidium formation. *B*, *P. purpurrescens* (Sopp) n. comb.: B_1, Camera lucida drawings of sterigmata and conidia; B_2, Diagrammatic representation of conidium formation in the same species. *C*, A type of conidium formation occasionally seen in various Penicillia and usually observed, as shown, in a strain, NRRL 1129, assignable to *P. tardum* Thom: C_1, Camera lucida drawings of sterigmata showing origin of conidia from cup-like tubes; C_2, Diagrammatic representation of this type of conidial origin. *a*, Conidium bearing tube of sterigma; *b*, Young conidium in formative stage; *c*, Connective, disjunctor, or bridge consisting of an extension of the primary wall from one conidial cell to the next; *d*, Secondary, more or less thickened wall; and *e*, Primary wall closely applied to secondary wall in A_2 and C_2, in B_2 it becomes pushed out somewhat as coloring substance accumulates between the outer (primary) and inner (secondary) walls. See discussion in text.

Corda, in describing and illustrating his *Penicillium fieberi*, specified that the oldest (or end) conidium of the chain, and sometimes the second oldest conidium, was much larger than the others. This condition has seldom been reported by subsequent workers although Biourge reported the "phenomenon of Corda" for a few species. Thom (1930) observed, in a culture belonging to the *P. brevi-compactum* series, a condition which he thought probably constituted the basis for Corda's interpretation. Drops of fluid were exuded at various points in the penicillus and along the conidial chains in such a way that the conidia at the very tips seemed to be much larger than those subsequently developed. More recently Swift

(1935) has reported the terminal conidium in *P. bacillosporum* to be fairly consistently larger in diameter and of somewhat different shape. Raper and Fennell (1948), in their description of *P. levitum* n. sp., have likewise noted that the terminal conidium is often substantially larger than other cells in the same chain. There is, however, no evidence that either of these species might represent Corda's *P. fieberi*.

Conidia may remain connected in chains of varying length, or may fall away quickly. Chains of conidia may diverge widely, become a tangled mass, stand almost rigidly parallel, or be closely aggregated into columnar masses. In certain species such masses may form continuous crusts covering large areas of the colony. In any case, the same general arrangement of conidial chains in the mass is usually recognizable in successive cultures for each species studied.

Conidium Formation

The method of conidium formation (fig. 12): was discussed by Thom in 1914 and more recently by Scaramella (1928). Thom described the newly formed conidium as at first a cylindrical segment cut from the conidium bearing tube at the tip of the sterigma. It attained the size and shape characteristic of its species by lengthening and swelling, and by the formation of its own cell wall within the primary wall which he regarded as derived from the parent cell or sterigma. The new wall, or true conidium wall, might blend with the primary wall to leave no visible line of separation, or it might only partially combine with the old wall, leaving a bridge or connective easily visible between successive conidia in the chain. Again, also as in *Aspergillus*, there may be a wrinkling of the old wall to form ridges or spinulose points on the conidium, with or without some deposit of coloring substance between the two walls to give coarseness or body to the roughenings or spinulosities.

Another view, based upon the original discussion by Gueguen (1899), regards conidium formation as "endogenous," i.e., the separation of a spore mass within a mother cell in such a way that it is allowed to slip out through a tube. Theoretical differences between this process and the above are practically confined to cell wall relations, without seriously affecting the basic observations of either group of workers. In the latter case it is only necessary to assume that the tip of the conidium bearing tube becomes ruptured and somewhat recurved, and that subsequent conidia are formed after the establishment of a new membrane or wall adjacent to the inner face of the old tube wall.

In our experience over many years we have usually found conidium formation to follow closely the pattern described by Thom in 1914 (figs. 12A and 12B). Nevertheless, we have occasionally observed preparations

in which the conidia seemed to be formed within the sterigma tube as described by Guegen and as illustrated by Scaramella (1928) for *Penicillium digitatum*. Whereas the latter type of development may occur occasionally in other series of *Penicillium*, particularly in old sterigmata, it is most readily observable in strains of *P. digitatum* and in a strain regarded by us as representing *P. tardum* Thom (fig. 12C) but received from Professor Westerdijk as *P. scorteum* of Takeda, Suematsu, and Nakazawa (see p. 653). The latter type of conidium formation is strongly suggestive of the dematiaceous genus *Cadophora*.

Connectives

Once formed, the conidium reaches a characteristic shape and pattern by enlarging and laying down a new wall within the primary wall, which is continuous with that of the parent cell. The presence of the vestigial cell wall as a connective (fig.12): between conidia within the chain is common in some species and occasionally seen in others. This appearance has been referred to as a bridge, disjunctor, or connective by various authors, and considerable importance has often been ascribed to it. Thom, 1914a, showed it to be merely incidental to the formation of the thickened cell wall of the conidium itself, leaving occasional gaps between the new wall and the old when the rounding conidia drew apart in their development. The view that the connective represents an abortive cell was effectively disposed of by Thom in 1914a.

Size of Conidia

The measurements of conidia form a part of every species description. These are expressed in microns (μ), either as the diameter or range in measurement for globose series, or as the long axis by the short axis for elliptical or subglobose cells. In many of our strains, some of which have been kept in continuous culture for more than 40 years, measurements show a fairly consistent range of variation, hence afford a reasonable criterion for use in strain or species identification. In the ordinary microscopic field there are hundreds of conidia in which the range of measurements can be carefully observed and recorded together with the limits most frequently seen. Results may be expressed in various ways, preferably as a fairly narrow range of measurement covering the majority of cells, but often supplemented by additional figures to show the more complete variation encountered, especially if this is marked. Few lots of conidia fail to show a considerable range in diameter. Figures to the tenth of a micron, therefore, mean little unless the range of variation is indicated or implied. A series of figures clearly setting forth the range of dimensions encountered is worth immeasurably more than a precise value

obtained by averaging the dimensions of a large number of cells. In the study of the Penicillia the occasional presence of a greatly enlarged conidium, among hundreds that are reasonably uniform in size, scarcely warrants increasing the range of measurements reported for conidia of the usual diameter. Such observations do suggest, however, a need for further study to account for the contrast in size. In some cases such enlarged cells may represent conidia in early stages of germination. In other cases they undoubtedly result from an interruption of normal septation at the tip of the sterigma in such a way that the material normally going into two or more conidia becomes contained within a single cell wall.

Germination of Conidia

When inoculated into a favorable nutrient, conidia tend to germinate in a manner essentially characteristic of the species under examination. In some species conidia swell greatly before putting out one or more germ tubes; some merely "round-up". Furthermore, the number and arrangement of germ tubes may be fairly characteristic in some species and not at all characteristic in others. In the genus *Scopulariopsis*, oftentimes regarded as related to *Penicillium*, a single germ tube arises only from a special area or germinal pore at the base of the conidium. In *Penicillium* germ tubes generally seem to be able to arise at almost any point on the cell surface.

SCLEROTIA

Sclerotia are characteristic of certain series and species of *Penicillium* (fig. 13). However, no particular taxonomic significance comparable to that observed in the genus *Aspergillus* can be attributed to their presence. The latter genus can be separated into two main parts upon the criterion of whether or not sclerotia are produced. In the genus *Penicillium*, series producing sclerotia are observed in each of the three major sections. Among the Monoverticillata the production of elliptical to globose sclerotia is regularly characteristic of members of the *Penicillium thomii* series. Typically these consist of very hard masses of pseudoparenchymatous tissue in which the walls of individual cells are very thick. Similar sclerotia are seen in *P. raistrickii* in the Divaricata, and a considerable degree of relationship to the *P. thomii* series is suggested. In *P. turbatum*, of the *P. thomii* series, and in *P. soppi*, of the *P. raistrickii* series, small, soft masses of thick-walled cells usually develop (fig. 75). These hardly represent true sclerotia in the sense of *P. thomii* and *P. raistrickii*, but their presence is accepted as evidence of relationship to these species, hence their assignment with them.

Rounded, firm sclerotia are also produced in *Penicillium gladioli* (fig.

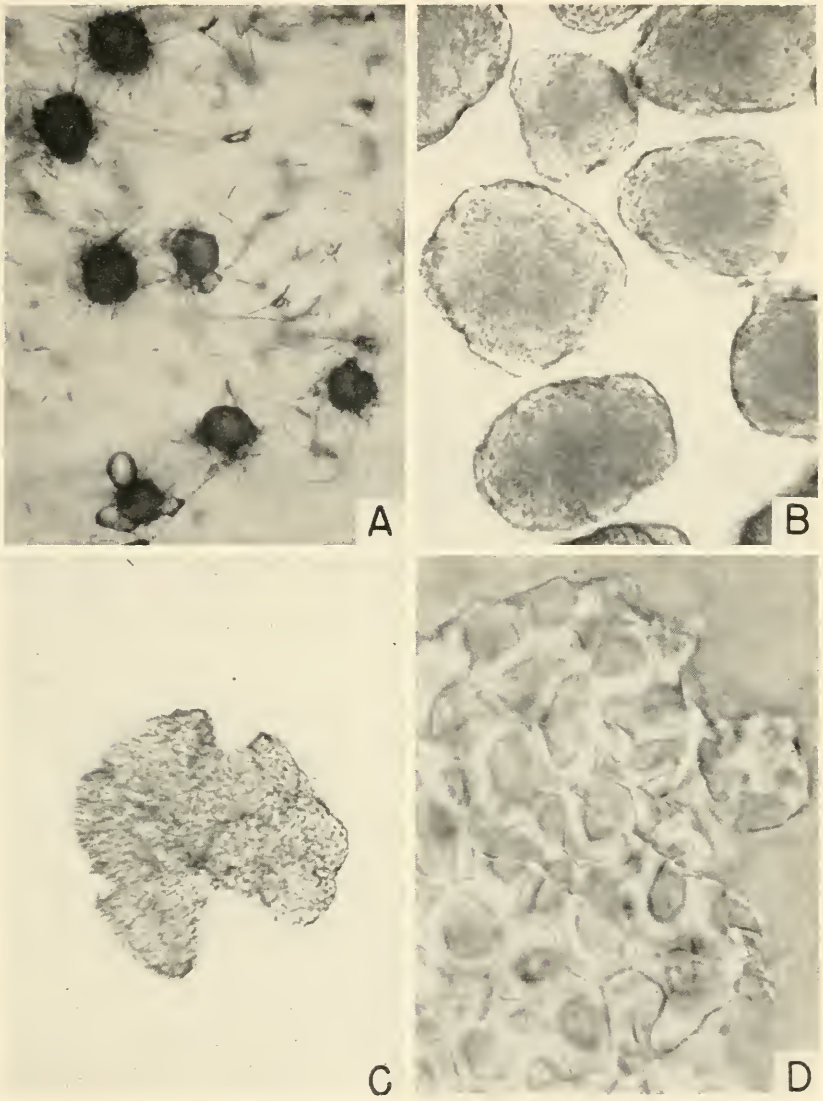


FIG. 13. Sclerotia in *Penicillium raistrickii* Smith. *A*, Low power view, × 55. *B*, Enlarged view showing general contours, × 105. *C*, Single sclerotium crushed, showing irregular manner of breaking. *D*, Enlarged view of small area showing detail of the thick-walled cells which comprise the sclerotium, × 725.

122), a species of the Fasciculata, and are occasionally seen in *P. italicum*, the blue-mold rot of citrus fruit.

A different type of sclerotium is produced in certain members of the Biverticillata-Symmetrica. In *Penicillium novae-zeelandiae*, for example,

the sclerotia are elongate and consist of a compact mass of dark, thick-walled cells. In contrast to the sclerotia already described which are borne upon the agar surface, those of *P. novae-zeelandiae* are as a rule wholly or partially buried within the substratum (fig. 167). Sclerotia of the same general type are occasionally encountered in strains of *P. funiculosum* and are characteristic of Thom's *P. purpurogenum* var. *rubrisclerotium*.

PERITHECIA

Perithecia regularly occur in three separate series, one of which occurs in each of the three major sections of the genus *Penicillium*. The presence of perithecia, therefore, while it constitutes our best basis for diagnosis and separation of individual strains and species, cannot be considered as characteristic of any major part of the genus and not of others. In general, two markedly different types of perithecia are produced.

In the *Carpenteles* series, and to a greater or less degree in the *Penicillium javanicum* series, the perithecia first develop as masses of thick-walled cells strongly suggestive of sclerotia (fig. 14). These subsequently produce ascospores by a process of differentiation and maturation which begins first at the center of the body and gradually progresses outward. In some cases ripe ascospores may appear within a week to ten days. In others, the development of such ripe spores may require a month or more. The general type of perithecium found here was described in considerable detail by Brefeld in his study of "*P. glaucum*" in 1874. Half a century later, in his study and description of *P. brefeldianum*, Dodge (1933) discussed the origin and development of a perithecium of the same general type and considered at length the formation and ripening of asci and ascospores. The subject was further elaborated by Emmons (1935) in his study of ascocarp formation in the genus *Penicillium*. The reader is referred to these original papers and to our general discussions at the beginning of the *P. javanicum* and *Carpenteles* series, respectively.

In the *Penicillium luteum* series the perithecium develops in an entirely different manner (fig. 15). A loose network of specialized hyphae develops which may or may not be surrounded by a protective covering or peridium. If such a covering appears, it usually consists of a loose network of interlacing, highly pigmented hyphae usually bright yellow in color. In a few cases these may become sufficiently compacted together to form a membranous sheath or envelope. Emmons (1935) reported and illustrated the type of perithecial initials present in the species examined by him (fig. 16). In the present study we have confirmed his observations, almost without exception, and have included observations on some additional new species. Great variability is shown (see fig. 144), and some question exists as to

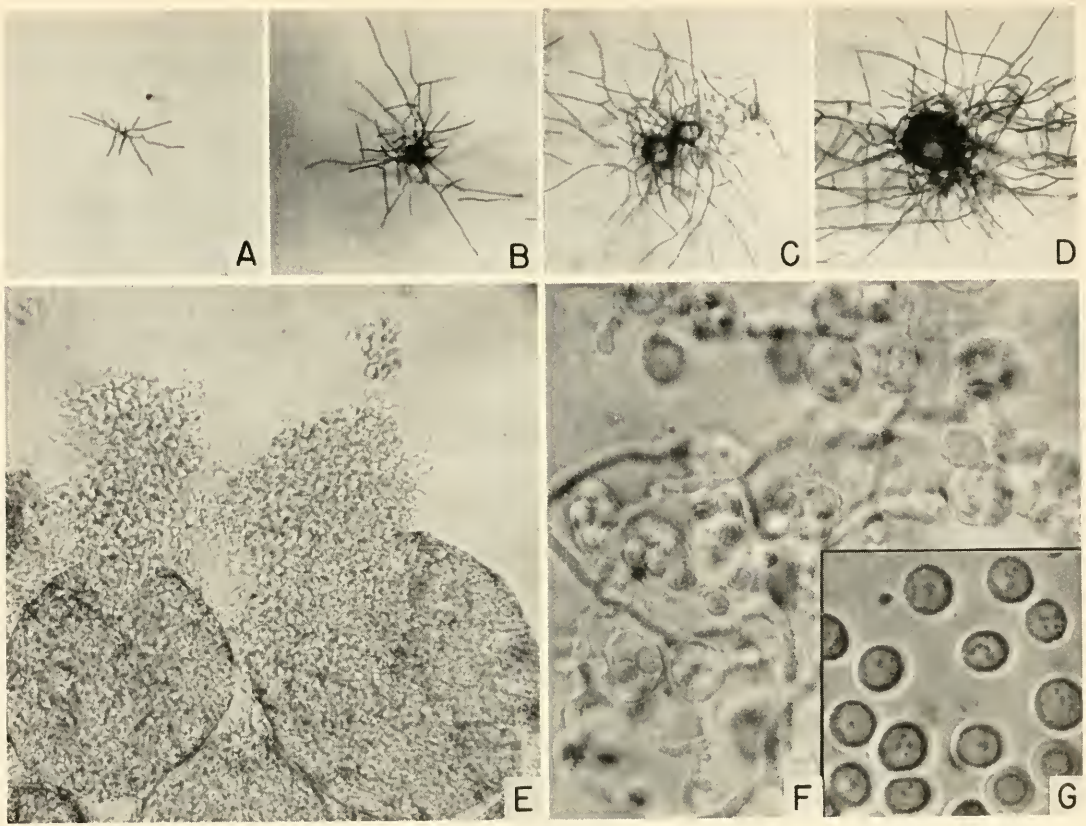


FIG. 14. Pattern of perithecium development in *Penicillium levitum* Raper and Fennell, representative of the *P. javanicum* and *Carpenteles* series. *A–D*, Successive stages in perithecium formation, × 40. *E*, Perithecia crushed sufficiently to push out masses of fertile hyphae, asci, and ascospores, × 185; note the intact cellular perithecial wall, or peridium. *F*, Asci in various stages of maturity, × 800. *G*, Ripe ascospores, × 1500.

the homogeneity of the *P. luteum* series as a natural group. For the present, however, we believe it is wise to hold together in one place all asco-

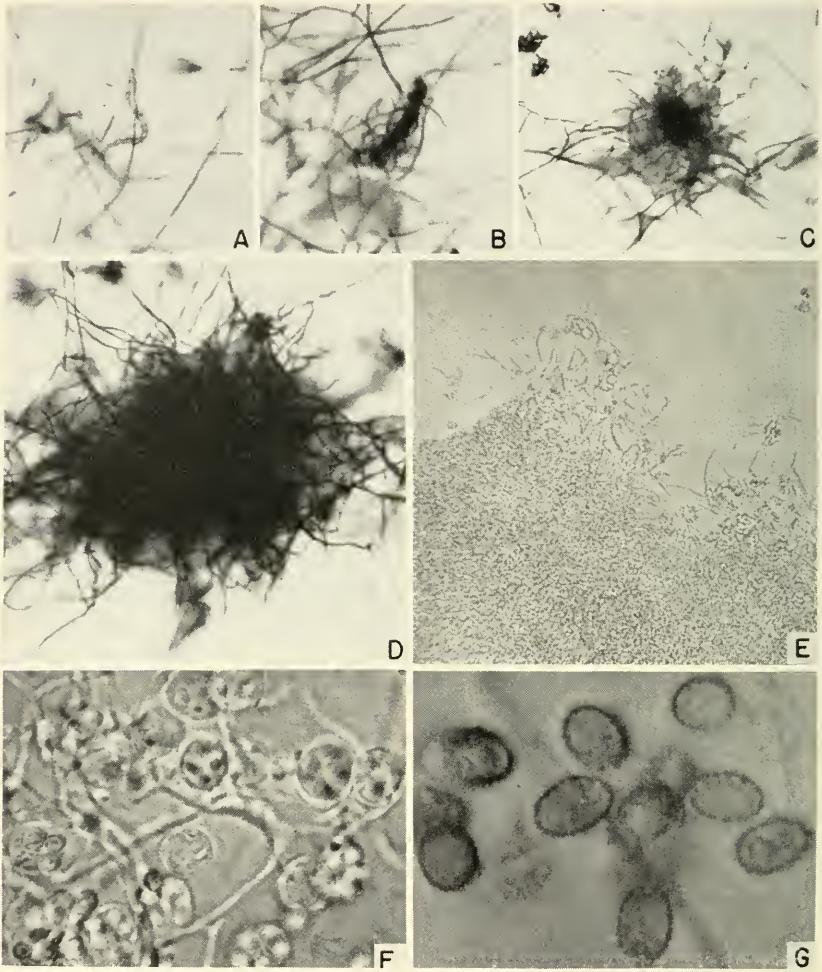


FIG. 15. Pattern of perithecium development in *Penicillium vermiculatum* Dangeard, representative of the *P. luteum* series. *A–D*, Successive stages in perithecium formation, magnified about 100 times. *E*, Perithecium partially crushed with asci being expelled, and showing the loose character of the body and the absence of any definite peridium, × 190. *F*, Asci in varying stages of maturity, × 800. *G*, Ripe ascospores, × 2400.

sporic species of *Penicillium* producing soft, loose-textured perithecia. The reader is referred to Emmons' paper (1935) and to our discussion of the series (pp. 564–573) for details of structure and development in the

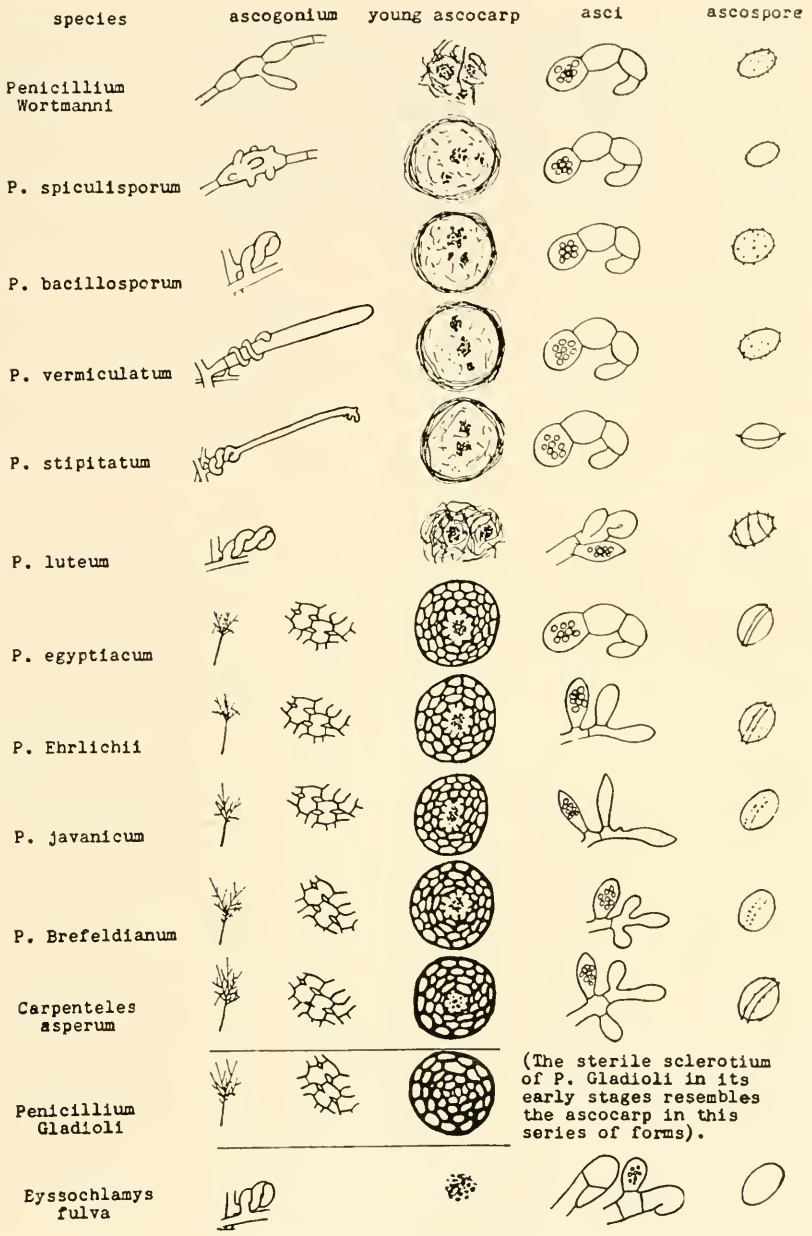


FIG. 16. Emmons' diagram showing the pattern of perithecial initials, the character of perithecia, the origin of asci, and the form and markings of ascospores in various species of *Penicillium* and in *Byssochlamys fulva*. (After Emmons, Mycologia *27*, 1935.)

different species included. The perithecia in this series merge imperceptibly into ascosporic structures of the type usually included in the genus *Gymnoascus*. Derx (1925–1926) reported a strain of *P. lutcum* to be heterothallic, but this has not been confirmed by subsequent investigators. Emmons in 1935 tested each of the ascosporic species studied by him and reported all of them to be homothallic. During the past few years a considerable number of ascosporic Penicillia have been described and a thorough study of these forms, extending the excellent work of Emmons, should be undertaken.

The discovery of perithecia in any culture greatly facilitates the identification of that form. We cannot, however, place primary emphasis upon the presence or absence of such structures in the taxonomy of the genus *Penicillium*. The student of these molds still requires a means of identifying conidial forms which continue to constitute 90 per cent or more of the organisms which appear in his cultures.

CYTOLOGY

Gueguen in 1898–1899 reported work upon the cytology of *Penicillium glaucum*. Cultures upon moist bread were taken as normal. Best results were obtained without fixation. The conidial wall was reported to be comparatively thick, representing one-fifth of the total diameter, and showed in optical section alternate areas thin and re-inforced, hence staining differently. The old spore wall was seen and figured on the remains of the swollen cell in contrast to the thin wall of the growing hypha in the germinating conidium. He depended upon intravitum staining with gentian violet or dahlia in very dilute solutions. Vegetative cells were reported to be multinucleate, and the cells of the conidiophore were not different in structure from those of the vegetative hyphae. The branches and metulae were also multinucleate. He figured the young sterigma as at first multinucleate, the actual number being variable, then reduced (fusion is suggested) to two, one of them centrally located, the other at the point of conidium formation. Although two nuclei are figured in the sterigma and the conidium in the process of separation, he reported only one nucleus in the conidium when separation was complete. His inference was that before the wall was laid down, one of the two nuclei in the developing conidium migrated back to the apical position in the sterigma to become the nucleus of the next conidium and to be replaced at the apex of the sterigma by another produced by division of the central nucleus. Multinucleate conditions were resumed in the process of germination.

More recently, Baker (1944a and 1944b), studying the cytology of *Penicillium notatum*, reported the conidia to be usually uninucleate or occasionally binucleate. A single conidium can develop into a typical

conidium-bearing mycelium. Such a colony is regarded as homotypic if the parent conidium was uninucleate, or heterotypic if the conidium was binucleate. In any case, wherever two or more conidia are involved, branches of the different mycelia quickly anastomose to establish a heterokaryotic condition in the developing mycelium. The regular development of anastomoses resulting in heterokaryotic mycelia in *P. notatum* is likewise reported by Pontecorvo and Gemmell (1944a) and by Lindegren and Andrews (1945).

Chapter IV

CULTIVATION AND PRESERVATION OF PENICILLIA

A few species of *Penicillium*, such as *Penicillium roqueforti* Thom, *P. camemberti* Thom, *P. expansum* Link, *P. italicum* Wehmer, and *P. digitatum* Sacc., are so closely associated with particular products or processes that the presence of a *Penicillium* in such situations warrants presumption of identities which are usually confirmed by microscopic examination. The majority of the Penicillia, however, have not been shown to bear any specific relation to particular processes or products. Such organisms appear as part of the complex population of stale or decaying organic matter. Almost any species of *Penicillium* can be isolated from soil, and certain species are usually present in considerable abundance. From the numbers present, as determined by dilution platings and other laboratory techniques, they are sometimes assumed to play an important role in soil decomposition processes. As a rule, however, there is little experimental evidence to support such assumptions.

The descriptions of Penicillia found in the literature up to the beginning of Wehmer's work were almost invariably based upon the microscopic examination of preparations made from selected spots in naturally moldy products. Representatives of other genera were usually intermixed. As early as 1890 Sopp reported that he found the current descriptions of Penicillia unsatisfactory, hence turned to laboratory culture as the best hope for a stable nomenclature.

Culture Media

The development of artificial culture methods made possible the isolation and study of the habits of the individual mold. Along with the academic interest in mold itself, the significance of some of these molds as the active agents of decay, fermentation, or ripening activity gave such studies an increased importance. For the cultivation of Penicillia the media already developed in the study of Aspergilli, yeasts, and bacteria were first utilized. Most species of the group were found to grow readily upon any culture medium used for bacteriological or mycological work.

Naturally, for organisms growing so readily, students of *Penicillium* have usually employed formulae already in use in their laboratories, except as particular purposes called for the development of specific combinations. Every kind of medium has, therefore, been used and work has been recorded upon many different nutrients. Certain formulas have, however,

been extensively used in the description of species of this group and these will be more or less fully discussed.

MEDIA USED IN EARLIER STUDIES

Raulin's Solution

The following solution, proposed by Raulin (1869) in his study of the biochemical activity of *Aspergillus niger*, has been widely used:

Water	1500.0 grams
Cane sugar	70.0 grams
Tartaric acid	4.0 grams
Ammonium nitrate	4.0 grams
Ammonium phosphate	0.6 grams
Potassium carbonate	0.6 grams
Magnesium carbonate	0.4 grams
Ammonium sulphate	0.25 grams
Zinc sulphate	0.07 grams
Iron sulphate	0.07 grams
Potassium silicate	0.07 grams

Dierckx's neutral Raulin's fluid as given by Biourge (1923, p. 43) follows:

1. Magnesium carbonate ..... 0.40 gram
   Tartaric acid ..... 0.71 gram
   Triturate in a mortar with a few drops of distilled water and add quickly to a flask of distilled water; make up to 100 ml.

2. To a liter flask with 800 to 900 ml. distilled water add:

Sucrose	46.60 grams
Ammonium nitrate	2.66 grams
Ammonium phosphate	0.40 gram
Potassium carbonate	0.40 gram
Ammonium sulphate	0.16 gram
Zinc sulphate	0.04 gram
Iron sulphate	0.04 gram

3. Add 66 to 67 ml. of the magnesium tartrate solution (1) to the mineral salt-sucrose solution (2) and make up to 1,000 ml. with distilled water.

Biourge (1923) noted that the purpose of this revision was to eliminate the free tartaric acid of Raulin's original formula by using only enough to dissolve the magnesium carbonate. He appended in a note that he used 0.27 gram magnesium carbonate and 0.40 gram tartaric acid and ground these in a mortar with a few drops of water until dissolved, then diluted at once to a large volume to stop crystallization. Biourge regarded this as a good substratum when 10 percent gelatin was added, but as an indifferent or even poor nutrient when agar was used to produce a solid medium.

Zaleski (1927) used the same basic formula in describing his species, but

modified the method of preparation as follows (freely translated):

The tartaric acid crystals were shaken in lukewarm distilled water and let stand until dissolved. The magnesium carbonate was then added and dissolved at once. The ammonium salts were dissolved in separate vessels with the water slightly warmed. The rest of the components were dissolved together in about 300 cc. of water. The gelatin or agar was dissolved separately in about 500 cc. of water. After the gelatin or agar was fully dissolved, the other solutions were added while the mass was stirred. No precipitate formed when the mixture was properly made. No filtration or clearing process was needed with high grade gelatin. The gelatin medium was sterilized in steam on the first and third days. Agar media were autoclaved. Layers of substratum 4 to 5 mm. deep were used in the petri dishes.

Biourge sometimes used 0.75 percent of agar-agar and 5 percent of gelatin with this solution to prepare a solid substratum for general culture work with saprophytic molds. Zaleski made his solid substratum by adding 1.5 to 1.7 percent of agar-agar or 10 percent of gelatin.

Bean Agar and Potato Agar

Thom, in his "Cultural Studies" (1910), used potato agar and bean agar with and without sugar. The method of preparation follows:

Bean agar. The directions for making bean decoction were obtained from Mazé at the Pasteur Institute in Paris. Common white beans were heated in five volumes of water. Boiling was stopped just before the swelling of the cotyledons ruptured the seed coats. This gave a clear, slightly yellowish liquid which filtered readily, yet contained sufficient nutrients to grow many species normally. Agar was added as desired. Since this decoction is poor in available carbon, the addition of sugar was often desirable for many species.

Potato agar. This medium was selected because of its use in many mycological laboratories. The potatoes were carefully washed, pared, and sliced, then slowly heated for about two hours in approximately two volumes of water. At the close of the heating the water was allowed to boil. The whole was then filtered, water being added to make up the losses from evaporation and filtering. To this was added 1 per cent of shredded agar. It was then heated for from twenty to thirty minutes in the autoclave at 120°C. or higher, after which it was ready for use. If cloudy, it was refiltered through absorbent cotton. Titration showed that the medium was nearly neutral to phenolphthalein; consequently it was used without neutralizing. Uniform composition was not claimed, but cultures of the same species grown upon successive lots of this medium showed negligible differences in morphology.

Potato-Dextrose Agar

This medium, which is probably more widely used by plant pathologists than any other, will support good to luxuriant growth of most species of *Penicillium*. Colonies, however, generally fail to develop well marked cultural characteristics of a type useful in separating species. It has not, therefore, occupied a prominent place in the taxonomic literature of *Penicillium*. As in the case of corn meal agar, many different methods of

preparation have been reported with consequent variation in the richness and texture of the resulting media. The preparation marketed by the Digestive Ferments Co. (Difco) may be regarded as representative. It contains the following ingredients: Infusion from 50 grams dried potatoes; 20 grams dextrose; and 15 grams agar per liter of water. The pH should approximate 5.6.

Licorice Sticks

In his descriptions, Bainier failed to specify the type of culture vessel employed or the substratum upon which his cultures were grown for diagnostic observations. However, many references are made in his discussions to the use of licorice sticks for culture purposes. The cultures seen in his laboratory in 1905, and others received from Gueguen at his laboratory, were grown upon licorice sticks in constricted tubes containing water. Only such essential data regarding colony characters as could be made upon these licorice sticks is presented in Bainier's papers, hence we assume their routine use in his hands. This limitation adds greatly to the difficulty of interpreting his descriptions. Cultures upon licorice sticks grow well and maintain their vitality for a long time, but in our experience have proved exceedingly unsatisfactory in separating organisms closely related in the various groups.

Prune Gelatine

Westling's descriptions (1911) were based upon an infusion of about 10 prunes to a liter of water. To this he added 15 percent gelatine to produce a mass firm enough to be handled in petri dishes. Our own cultures with this medium were entirely satisfactory for general purposes, but we abandoned the formula because it cannot be defined accurately enough to insure uniformity when prepared in widely separated laboratories. The complexity of the nutrients present nullifies its value for biochemical studies. At best it has no advantage over the wort type of culture medium.

Wort or Beer Wort

Brewery wort, or beer wort, formed the basis of much of the media used by Wehmer, Sopp, Dierckx, Lindner, Biourge, and many other workers. Few of them specified the characteristics of the basic nutrient. Biourge (1923) alone offered some general limitations.

Wort according to Biourge. Select a pale wort (from the brewery) before the addition of hops, autoclave for fifteen minutes at 115 to 120°C., filter in the boiling condition, distribute in tubes or flasks, and sterilize fifteen minutes at 120°C. The density at 4.8°C. to 4.6°C. should be 12 to 14° Balling.

Wort-gelatine-agar according to Biourge. Biourge prepared his wort-gelatine-agar substratum by dissolving 1.5 per cent of agar-agar in the wort, autoclaving at 120°C. for a half hour, then adding an equal quantity of wort containing 10 per cent of gelatine, and sterilizing the mixture at 110°C. for fifteen to twenty minutes. Biourge's latin diagnoses appear to have been based upon cultures made with this substratum.

Both Sopp and Biourge regarded wort in some variety as a standard substratum for Penicillia, and it may be so regarded if reference is made merely to a substratum in which almost any *Penicillium* will grow. Wort and allied substances, however, are chemically very complex, and analyses of biochemical activities based upon reactions obtained are very difficult to determine. It is not uniform in successive lots or in different laboratories, and the color of the wort itself masks color reactions produced by many fungi. Nevertheless, it is very useful, especially for maintaining stock cultures of certain species which do not thrive upon synthetic media.

MEDIA USED IN THE PRESENT STUDY

Czapek's Solution Agar

Our collaboration with chemists upon the study of the biochemical activities of molds very early pointed to the desirability of a basal culture solution whose components were readily available in the stock room of any chemical or mycological laboratory. For this purpose Dox (1909) selected the general combination of reagents attributed to Czapek. The selection was intended to present each element in a single form as nearly as possible, thus permitting the elimination or substitution of single components and the determination of their significance in metabolism.

Water	1,000 cc.
$NaNO_3$	3.0 grams
K_2HPO_4	1.0 gram
$MgSO_4 \cdot 7H_2O$	0.5 gram
KCl	0.5 gram
$FeSO_4 \cdot 7H_2O$	0.01 gram
Sucrose (Cube or other good commercial grade)	30.0 grams
Agar	15.0 grams

To reduce caramelization the sugar is added just prior to final sterilization.

Culture data upon Penicillia grown in this type of medium have been accumulating in our laboratories since about 1909. In general, it cannot be claimed to be an optimum solution for Penicillia, but with a limited number of exceptions the species studied will grow and produce characteristic colonies upon such media. Oftentimes, failure to grow well becomes a negative character of great usefulness. Transfer back to Czapek's solution agar, from whatever other culture medium we have tried, has usually brought back the colony characters originally recorded. Such a synthetic

and reproducible medium gains a decided advantage to the describer so long as the growth obtained has well-marked characters and maintains the vigor of the strain of mold studied. In his Monograph, Thom (1930) based descriptive data almost exclusively upon this medium. In the present study species diagnoses are centered upon the same substratum, with supplemental data supplied from other media, particularly malt extract agar and a steep liquor enriched Czapek's solution referred to as "steep agar." The markedly different growth response exhibited by certain species and strains when cultivated upon these different substrata is strikingly shown in figure 17.

In making Czapek's solution agar the neutral potassium phosphate is preferred to the acid form of the salt, since with the neutral salt the final reaction of the medium is neutral or only very slightly acid, showing a reaction of pH 6.8 to 6.9. Opinions differ, and many workers prefer the medium of lower pH resulting from the use of the acid salt. Czapek's solution agar is not offered as an optimum substratum for any particular species, but as a mixture approximately neutral in reaction, which is readily made in any laboratory in fairly uniform manner, and which permits moderately vigorous growth of nearly all saprophytic Penicillia. The quantities of mycelium and conidia produced by many forms in other media are much greater; but for comparative study in the majority of the species a moderate growth is generally more useful than the great masses of mycelium and conidia which are readily obtained by using richer substrata.

Substitution of glucose for sucrose provides a medium which is more favorable for certain strains and species.

Czapek solution agar containing 20 percent, rather than the usual 3 percent sucrose, is routinely used for cultivating members of the *Aspergillus glaucus* group (see Thom and Raper, 1941). The same high sugar medium is occasionally very useful for securing conidial structures in certain species and strains of *Penicillium* which sporulate very lightly or not at all on standard Czapek agar. In a few cases, *e.g.*, *Penicillium levitum* Raper and Fennell, descriptive notes from this medium are incorporated into the species diagnosis.

In their earlier studies on the biochemistry of micro-organisms, including many different species of *Penicillium*, Raistrick and co-workers generally employed a modified Czapek-Dox solution in which 5 percent glucose was substituted for 3 percent sucrose and the $NaNO_3$ was reduced from 0.3 percent to 0.2 percent. More recently, beginning in 1932, they have commonly employed a modified Raulin's solution referred to as "Raulin-Thom medium" in which glucose is substituted for sucrose and potassium silicate is omitted (see Clutterbuck, *et al.* Biochem. Jour. *26:* 1444. 1932).

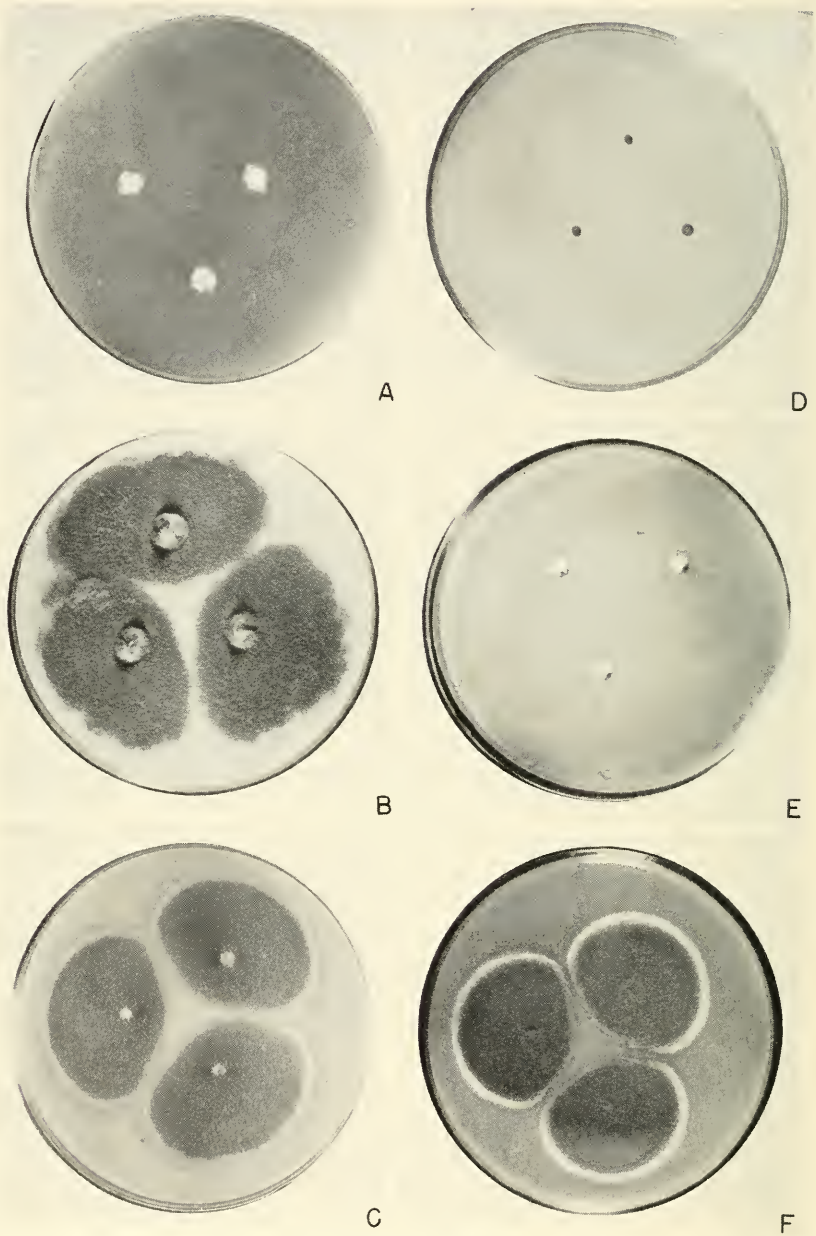


FIG. 17. Influence of substratum. *A–C, Penicillium digitatum* Saccardo, NRRL 1202, growing upon Czapek's solution, steep, and malt extract agars respectively; 10 days, 25°C. (see discussion p. 386). *D–F, P. diversum* Raper and Fennell, NRRL 2121, growing upon the same media under similar conditions (see discussion p. 653).

Steep Agar

This medium is prepared by adding to a standard Czapek's solution 1 percent of concentrated corn steep liquor. The pH is adjusted to 7.0 with normal NaOH prior to the addition of 1.5 percent agar. The medium is sterilized in the same manner as Czapek's.

Steep agar, as this enriched substratum is called, is particularly useful in the study of Penicillia since many species make a fairly luxuriant growth without losing characteristic colony patterns as on malt agar. Used in conjunction with standard Czapek's agar, the medium is likewise useful for revealing vitamin and other nutritional deficiencies since certain species and strains that grow sparsely and atypically on Czapek show a normal and luxuriant development on steep agar. In the present study we have made it routine practice to incorporate into specific diagnoses supplemental notes made from this medium.

Modifications of Czapek's solution agar involving enrichment with one percent yeast extract, one percent peptone, or one percent hydrolyzed casein instead of steep liquor result in media that produce colonies essentially similar to the above in rate of growth, texture, pigmentation, and spore production.

By substituting other carbon sources for sucrose and other nitrogen compounds for $NaNO_3$, agar media suitable for the presumptive determination of certain nutritional deficiencies encountered in the Penicillia may be readily prepared.

Malt Extract Agar

After many unsatisfactory experiences with brewery wort, and confronted with increasing difficulties in obtaining it in America, Thom followed Blakeslee, in his study of the Mucors, in substituting an artificial wort made with dried malt-extract. For the present study we have employed a malt agar of a composition recommended by Blakeslee (1915) as follows:

Malt extract (Difco)	20.0 grams
Dextrose	20.0 grams
Peptone	1.0 gram
Agar	25.0 grams
Distilled water	1.0 liter

The agar is melted in water in the autoclave prior to the addition of the nutrients. The pH is approximately 4.7 and is not adjusted. Using 2.5 percent agar, the medium should set firm when sterilized in the usual manner.

Bacto wort and malt extract agars, as marketed by the Digestive Fer-

ments Co. (Difco), develop colonies usually approximating those produced upon the malt agar routinely used in this Laboratory.

Whereas malt or wort agars seldom produce colonies of Penicillia with pronounced cultural characteristics, hence are of limited value in diagnostic work, they do as a rule favor the development of abundant conidia. They are especially valuable in studying ascosporic species, for perithecia usually develop abundantly upon these media, whereas such structures may be limited or altogether lacking upon Czapek agar. Many Penicillia grow more rapidly upon malt agar than upon Czapek; others do not. Differential rates of growth, therefore, often provide clues to relationship and identity. All of these factors entered into our decision to supplement species descriptions with notes made from malt agar cultures. The principal reason for this, however, rests in the wide use of such media by mycologists and stems from our belief that certain species may appear more tangible if described from media with which users of the Manual are possibly more familiar.

Corn Meal Agar

The corn meal agar as used by plant pathologists is in general represented by the following formula given by Shear and Stevens (1913):

> "To 40 grams of corn meal add 1 liter of water. Keep in a water bath for one hour at a temperature of 58°C., never over 60°C. Filter through paper, add 1.5 per cent of agar flour, steam for one and one-half hours, filter, and tube. Autoclave for fifteen minutes at 115°C."

For the present study we have prepared corn meal agar in two different ways with equally good results: (A) Steep 50 gms. white corn meal (contained in a cloth bag) in one liter of distilled water for three hours at 60°C.; filter and make up to original volume; add 1.5 percent agar; and sterilize in the usual way. (B) The alternate procedure is to boil the corn meal for one-half hour and then proceed as above.

A stiffer corn meal agar may be made by using 100 grams of corn meal and 15 grams of agar to 1000 cc. of distilled water, and heating all ingredients in an Arnold sterilizer for forty-five minutes or longer, if necessary, to dissolve the agar. This medium is then handled without filtration and is sterilized by autoclaving.

Different laboratories using corn meal agar use quite varied quantities of corn meal to the liter of distilled water, and report the final unadjusted products as varying from pH 5.8 to 6.5. There appears to be in fact about as many kinds of corn meal agar as there are workers who use it.

Corn meal agar is especially useful for investigating ascosporic Penicillia. In such species perithecia in limited numbers are regularly produced and

the developing colonies are especially favorable for observing the earliest stages of perithecium formation (see fig. 144). Emmons (1935), Dodge (1933), Shear (1934), and Swift (1932), based their studies largely upon this substratum. In our present discussion, notes from corn meal agar cultures commonly form an important part of the diagnosis of ascosporic species.

Hay Infusion Agar

Hay infusion agar is very useful for isolating Penicillia from nature since it permits a great number of forms to make a limited growth without particularly favoring the development of any single species. Perithecia usually develop upon this medium, as on corn meal agar, if a strain exhibits any capacity whatever to develop an ascosporic stage. In certain species, such as *Penicillium javanicum* v. Beyma, the medium seems to favor more than most the development of conidial structures as well. Descriptive notes from hay agar cultures are incorporated into the species diagnosis of a few species in this Manual.

The medium is prepared as follows:

Distilled water	1000 cc.
Decomposing hay	50 grams
Autoclave for 30 minutes at 15 pounds.	
Filter.	
Infusion filtrate	1000 cc.
K_2HPO_4	2 grams
Agar	15 grams
Adjust pH to 6.2 ± before final sterilization.	

Wickerham's Antibiotic Test Medium

Penicillin production is characteristic of the *Penicillium chrysogenum* series. The production of citrinin is characteristic of *P. citrinum*. The production of claviformin is characteristic of several species of the Fasciculata, including *P. claviforme*, *P. urticae*, *P. expansum*, and others. While the production of these antibiotics cannot be taken as sole or conclusive proof of relationships, proof that one of them is produced often affords a strong indication of such ties. A simple, bacterial-spectrum test for (1) revealing the production of antibiotics and (2) differentiating between penicillin, citrinin, and claviformin has been successfully devised by our associate, Dr. L. J. Wickerham. This test consists of a simple determination of the relative inhibition of selected test organisms by growing mold cultures (see p. 75). It has repeatedly proved valuable in our present taxonomic studies, particularly in the assignment of strains showing the general morphology of *P. citrinum*. The culture medium upon which the mold cultures, and subsequently the bacterial test strains, are grown, has

the following composition:

Yeast extract	2.0 grams
Peptone	3.0 grams
Dextrose	2.0 grams
Sucrose	30.0 grams
Corn steep solids	5.0 grams
$NaNO_3$	2.0 grams
$K_2HPO_4 \cdot 3H_2O$	1.0 grams
$MgSO_4$	0.5 grams
KCl	0.2 grams
$FeSO_4 \cdot 7H_2O$	0.01 grams
Distilled water	1000 ml.
Agar	20.0 grams
Adjust before autoclaving to pH	7.0

Preparation of Cultures

Recognizing the necessity of laboratory cultivation, and assuming the availability of suitable media and culture facilities, the preparation of different types of cultures which are important in the study of the Penicillia will next be considered.

Two types of culture vessels, namely test tubes and petri dishes, should be constantly available in adequate numbers. Of these, the first is of particular importance for the maintenance and storage of stocks, whereas the latter is invaluable for the detailed observations of colonies and conidial structures upon which successful diagnosis depends. Tubes of any convenient size may be employed. In our work we have found tubes measuring 15 x 125 mm. to afford adequate space for limited culture development, and at the same time to conserve valuable storage space. Standard petri dishes, 10 cm. in diameter by 1.5 cm. deep, are used for most purposes. A larger dish, measuring 15 cm. by 2 cm., is very useful for dilution plates and for other types of cultures in which many colonies are to develop, or in which the worker wishes to observe individual colonies over an extended period.

TYPES OF CULTURES

Test Tube Cultures

The preparation of test tube cultures is practically essential in the handling of a *Penicillium*. Inoculation of such tubes is usually made by wire or loop from a selected mass of mycelium or spores. In studying specimens as received, or as newly isolated, transfers to test tubes should be made before any other studies are begun. This will perpetuate as nearly as possible the exact content of the original culture or specimen. Recultivation may ultimately show the original to be valueless, in which case the

primary tubes can be easily destroyed. If, on the other hand, such primary tubes are not made, subsequent studies may be seriously interfered with by contamination or accidents in handling. A half dozen tube transfers afford a measure of insurance out of all proportion to the time required for their preparation. Such tube cultures, however, cannot be recommended for observation: (1) the colony area is generally too small and too confined for the development of wholly characteristic cultural patterns; (2) the culture cannot be viewed directly with the low powers of the compound microscope; and (3) portions of the growing colony cannot be carefully selected and easily removed for the preparation of suitable microscopic mounts.

Plate Cultures

The success of taxonomic studies in the genus *Penicillium* hinges upon the cultivation of these molds in petri dishes where cultural and microscopical developments can be followed simultaneously throughout the growing period. Different types of plate cultures have special applications:

Spot Cultures: The type of culture most commonly employed is based upon the spot inoculation of agar plates with masses of conidia or bits of mycelium from a selected area in the parent culture. Such transfers can be made by means of a conventional wire needle or loop. For most work it is not necessary to have in the developing culture a particular number of colonies, although these should not be so numerous as to preclude the development of normal colony patterns. Where it is desired to establish a specific number of colonies in particular positions within the culture plate, it is advisable to suspend the conidia in water, or better still in melted agar, at about 45°C. and then transfer small amounts of the gelled spore suspension to the fresh culture. Single colonies are desirable for some types of observation and these can be established in the same manner. For most types of work, however, cultures showing two or more colonies are more useful. In such cultures one can study the mature growth and fruiting habits of the mold best in the area where the colonies approach one another, whereas their habits of vegetative growth can, at the same time, be studied at the opposite side of the colony where growth remains unrestricted. For our work we have found plates inoculated with three colonies to be generally satisfactory and to offer a degree of uniformity, useful for comparative purposes, which cannot be attained where either a single or an indefinite number of colonies develop.

Selection of the inoculum for this or other types of cultures to be subsequently considered, can best be accomplished with the aid of a 10X pocket magnifier or a wide field binocular microscope. Using the latter instru-

ment and a finely pointed needle fashioned from nichrome or platinum-iridium wire, conidia from a single or a few selected penicilli can be easily removed.

Slanted Plates: By using slanted plates one can, in a single culture, study the effects of varying depths of agar as this influences the rate of evaporation, the concentration of nutrients, and other factors which markedly effect the rate and pattern of colony growth. Biourge recommended the use of slanted plate cultures for some types of observation. Thom likewise used this type of culture in certain of his observations and called attention to the advantages and disadvantages inherent in it. The use of such non-uniform agar layers necessitates careful evaluation of the influence of all environmental factors.

Dilution Cultures: Dilution cultures are extremely useful in certain types of work, particularly the isolation of strains from soil or other natural substrata. They are equally useful for separating two or more Penicillia which may be growing in close association as a result of contamination. Two general techniques may be employed, both of which represent common bacteriological practices.

The first of these consists of suspending the inoculum or sample of natural material in a sterile water blank and diluting this progressively by the serial transfer of aliquots of specified amount, usually 1 cc., from one to another in a series of similar water blanks. Samples are removed from the dilutions selected as probably most suitable and placed in sterile petri dishes followed by the addition of a melted agar medium at about 45°C. In cultures developing from such dilution plates it is desirable to have not less than 3 colonies or more than 10 or 12.

The second method of preparing dilution cultures consists of adding the inoculum or sample to a tube of melted agar and carefully mixing the added material throughout the agar mass. By means of a pipette or loop, a small amount of this suspension is then transferred to a second agar tube, a portion of the second to the third, etc., to secure the desired dilutions of the original sample. The melted agar containing such dilutions is then poured into petri dishes and allowed to solidify. The second method is often equally as satisfactory as the first.

Streak Cultures: For isolating Penicillia from natural materials, or for separating two or more strains growing together in culture, streak plates are often quite satisfactory and are more easily prepared than either of the above types of dilution plates. In the preparation of streak cultures care should be taken in selecting the inoculum so that a minimum of extraneous material is included and the streaking process should be continued through a distance sufficient to allow the development of separate colonies. Oftentimes this requires that streaking from an original loopful of inocu-

lum be extended into a second plate. This method has special merit in separating molds from contaminating bacteria.

Streak cultures have another important application in the study of natural variation within an unstable strain of *Penicillium* since variant growth types have an opportunity to develop as separate colonies if the inoculum is representative of the parent culture. The same type of culture can be very useful when it is desired to obtain conidial structures suitable for microscopic examination *in situ* within two or three days.

Single Spore Cultures: Dilution of spores in sterile water, followed by plating in agar as described above, constitutes a satisfactory means of isolating "single" spore cultures where it is sufficient if 90 or 95 percent of the resulting colonies develop from individual conidia. That such a percentage actually develops from single cells can be determined by comparing the number of developing colonies with the haemocytometer count of conidia present in the original suspension. Using such cultures, however, it is impossible to know whether any particular colony developed from a single conidium, or from two or more adherent cells.

Where the investigator needs to know with certainty that every colony has developed from a single spore, it is necessary to employ some technique combining microscopic examination with a device or means for the mechanical removal of selected spores. This can be accomplished with the aid of some type of micro-manipulator with which individual cells are removed from a water suspension and subsequently transferred to a suitable culture plate or tube. It may also be accomplished by means of some type of cutting disk attached to a holder or frame which can be mounted in the nose-piece of the compound microscope and alternately swung into position and out again as described by Lambert (1939) and others. A somewhat simpler and more rapid method can be used when one is dealing with cells 3μ or more in diameter. Such a procedure has been developed and used extensively at this Laboratory. Briefly described, the method is as follows: Conidia of a selected culture are thoroughly dispersed in sterile water containing a detergent, sodium lauryl sulfonate, in a concentration of 1:10,000. Appropriate dilutions of this suspension are then spread evenly over the surface of a carefully filtered nutrient agar. The plates are incubated at a favorable temperature over night and the conidia allowed to germinate. The plates are examined on the following day with a wide field binocular microscope and the positions of isolated germinating cells are marked. These are then carefully checked with a compound microscope using an 8 mm. objective to insure that no ungerminated spores are present in the immediate area of the cells selected for isolation. By means of a micro-scalpel fashioned from thin platinum-iridium wire, a minute block of agar surrounding the se-

lected spore is removed under the low power binocular and transferred to a fresh agar plate. The small agar block is then re-examined with the 8 mm. objective to insure that the selected spore has been transplanted.

Spectrum Test Plates: The following procedure has been successfully used to demonstrate the production of antibiotics by species of *Penicillium* and other molds. Petri dishes are poured with 20 ml. of Wickerham's antibiotics test medium (see p. 69) and the surface of the agar plates allowed to dry for one or two days at room temperature. At the end of this period a loopful of a suspension of mold spores or mycelium is streaked across one side of the plate surface, and the culture incubated for four days at 24°C. Following such incubation, suspensions of selected test organisms are streaked across the agar at right angles to the mold growth. The reinoculated plates are then incubated at 30°C. for 24 hours, after which the zones of inhibition are read by placing the plate over a millimeter scale. The test organisms, which grow rapidly at 30°C., are used because of their varied physiological characteristics. They include: *Bacillus cereus* NRRL B-569, *Candida albicans* NRRL Y-477, *Bacillus subtilis*, smooth-form, NRRL B-558, *Staphylococcus aureus* NRRL B-313, *Salmonella schottmüelleri* NRRL B-119, and *Proteus mirabilis* NRRL B-400. The *Salmonella* and *Proteus* strains represent Gram-negative forms, hence are insensitive, or only slightly sensitive, to penicillin. *Candida albicans* represents a yeast-like form, hence could be expected to differ from the other test species used. The strains of *Bacillus subtilis* and *Staphylococcus aureus* are very sensitive to penicillin and in fact represent organisms commonly used for the assay of this antibiotic. The strain of *Bacillus cereus* while representing a Gram-positive form, produces a powerful penicillinase, hence is generally not inhibited by penicillin. The differential response of the test organisms to penicillin, citrinin, and claviformin makes possible the identification of these antibiotics.

When penicillin is produced, the growth of *Bacillus subtilis* and *Staphylococcus aureus* is markedly inhibited, but that of *Bacillus cereus* shows little or no inhibition due to the destruction of penicillin by the penicillinase (fig. 18C).

When citrinin is produced, *Staphylococcus aureus*, *Bacillus subtilis*, and *Bacillus cereus* are all markedly inhibited, since the production of penicillinase by the latter species does not effect the power of citrinin to inhibit this Gram-positive strain (fig. 18B).

When claviformin is produced, growth of all the bacterial species is markedly inhibited since this antibiotic is effective against Gram-negative as well as Gram-positive forms, and the yeast, *Candida albicans*, is inhibited to a limited degree also (fig. 18D).

Since the production and characterization of penicillin, citrinin, and

claviformin are discussed in other portions of the text, these subjects need not be considered here.

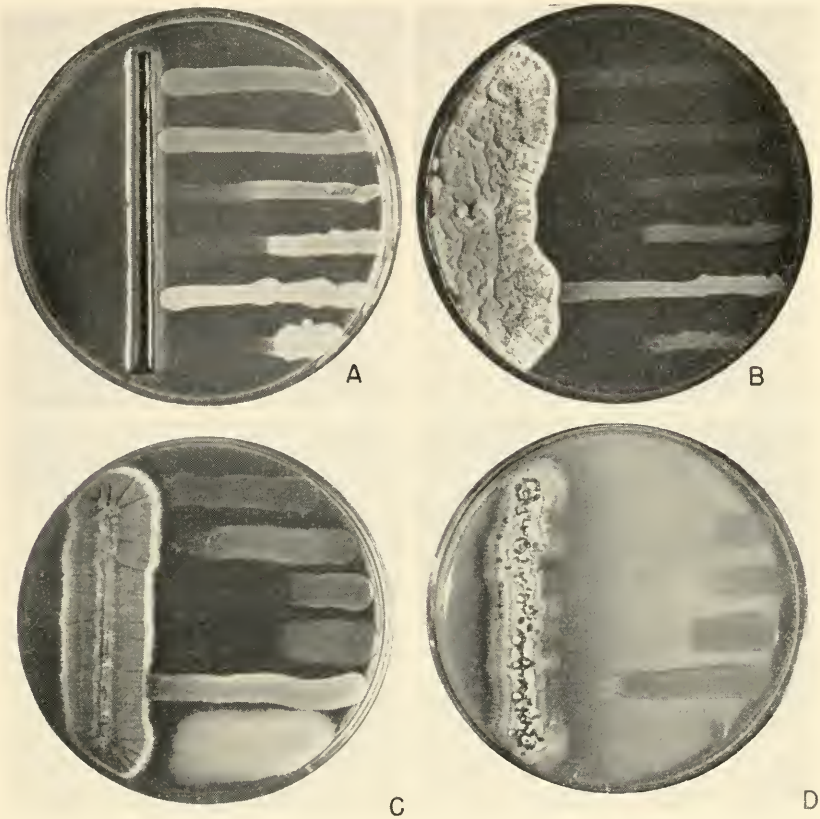


FIG. 18. Spectrum-plate method for the identification of antibiotic substances produced by Penicillia. *A*, Agar plate with trough containing solution of crystalline citrinin, showing the effect of this antibiotic upon the growth of six test microorganisms streaked as follows from top to bottom of the plate: *Proteus mirabilis*, NRRL B-400; *Salmonella schottmülleri*, NRRL B-119; *Staphylococcus aureus*, NRRL B-313; *Bacillus subtilis*, NRRL B-558; *Candida albicans*, NRRL Y-477; and *Bacillus cereus*, NRRL B-569. *B*, A plate similarly streaked four days after being inoculated with *Penicillium citrinum*, NRRL 1842. Note the identical patterns of inhibition in *A* and *B*. *C*, The same type of test in a four-day culture of a penicillin producing mold, *P. chrysogenum*, NRRL 1951.B25. *D*, The same type of test in a four-day culture of a claviformin producing mold, *P. claviforme*, NRRL 1002. See discussion in text, pp. 74–75.

Micro-Cultures

Ullscheck (1928) based his description of morphology upon cultures grown upon minute quantities of agar in slides manufactured for hanging drop studies. The culture chamber or depression was covered with a

sterile cover glass held in place by vaseline which was omitted along about one-fourth of the line of contact, thus insuring ventilation while remaining tight enough to exclude contamination and protect against evaporation. We have used similar apparatus in studying the germination of conidia, and specific types of morphology, but discarded it many years ago for the study of mature penicilli because of the atypical character of the structures produced as the colony developed beyond the germination stage. While growth is not as a rule quite so restricted, the same general objections apply to slide cultures as used by Henrici (1930, p. 30, figs. 25 and 26). The latter type of culture could, however, have limited application in photomicrography.

Incubation

temperature

Cosmopolitan saprophytes such as most species of *Penicillium* will grow well over a wide range of temperature. In general work, therefore, it is not necessary to provide special incubators. Thom, in 1910, reported that a range of from 15 to 25°C. produced differences only in the rate of development, not in the basic character of colonies. In our present study we have extended this range to 30°C. for many species and find that in the majority of cases the character of the colony still remains unaltered but that growth is oftentimes more rapid and sporulation often somewhat heavier. Less frequently, growth is reduced and sporulation decreased. Zaleski incubated his cultures at 16 to 20°C., whereas Biourge generally employed temperatures in the neighborhood of 18–20°C. For the present study we have used incubation temperatures of 23 to 25°C. except where otherwise noted. While this certainly does not represent the optimum temperature for individual species in all cases, we consider it to be a favorable range for most forms. We feel that a uniform incubation temperature is desirable for comparative purposes.

Certain species of *Penicillium* represent marked exceptions and behave very differently at temperatures above or below the level of 23–25°. McCulloch and Thom (1928) found *Penicillium gladioli* to produce abundant blue-green conidial structures when incubated at 14–15°C. The same species, when incubated at 22°C. or higher, produced comparatively few conidial structures but abundant hard sclerotia. *Penicillium duponti* represents a thermophilic species which grows luxuriantly upon most natural substrata at temperatures of 40–47°C. (fig. 19B). The same species makes a very limited growth at temperatures below this range and fails to grow at room temperature (fig. 19A). Strains of *Paecilomyces*, a genus generally regarded as related to *Penicillium*, grow quite well at

temperatures of 37–40°C., as do also species of *Scopulariopsis* which are often reported as parasitic to animals including man.

Our experiences indicate that the temperature of incubation should be a part of the record in every cultural description. In the present Manual this practice has been followed, the temperature being recorded either as 24°C., or as "room temperature," which in our air-conditioned Laboratory generally ranges from 23° to 25°C.

ACIDITY

Most species of *Penicillium* grow best in a mildly acid substratum. Usually, such a favorable reaction is established by the mold itself as it

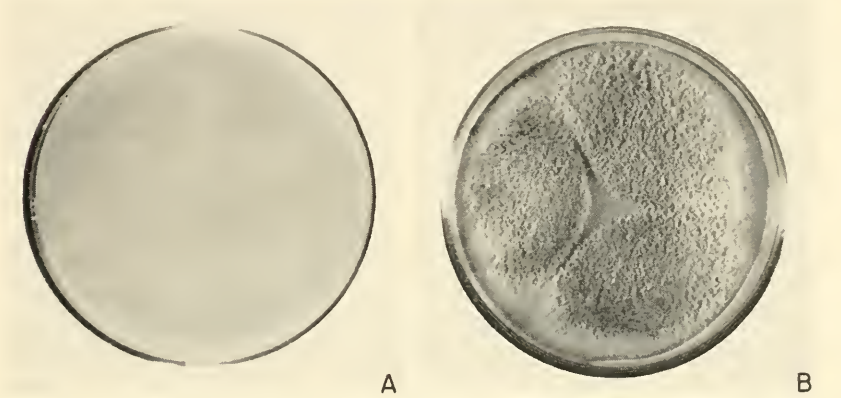


FIG. 19. Influence of incubation temperature. *Penicillium duponti* Griffon and Maublanc emend. Emerson, NRRL 2155, a thermophilic species. *A* and *B*, similarly inoculated plates incubated at 25° and 45°, respectively. Steep agar, 10 days. Note complete absence of growth in *A* and luxuriant growth in *B*.

decomposes whatever sugar or carbohydrate is supplied in the substratum. When Czapek's solution agar containing sucrose is employed, the usual course of development is as follows: The substratum is initially near neutrality or slightly acid, and with the ensuing growth of the mold shifts quickly to acid as the sugar is used up, then returns to neutral or becomes alkaline as relatively greater amounts of nitrogenous materials are broken down, often including the proteinaceous substance of the mold itself.

In certain species the response to acidity is very striking. *Penicillium digitatum* Sacc. grows very sparsely and restrictedly upon the standard Czapek solution agar (fig. 103C), but if the reaction is lowered to pH 4.0 fairly luxuriant growth is obtained. To a lesser degree, the same phenomenon is observable in *P. italicum* Wehmer. Both species represent active rots of citrus fruit, hence we can assume that their behavior in culture results from long conditioning and adaptation to their natural habitats.

In *Scopulariopsis*, a genus of molds often regarded as closely related to *Penicillium*, an entirely different response is often noted. In many strains, growth is poor or negligible upon malt agar that is strongly acid in reaction but fairly luxuriant upon substrata approximately neutral in reaction. The same response is seen in *Penicillium albicans*, a species suspected of being closely related to *Scopulariopsis*.

HUMIDITY

In cultivating the majority of Penicillia on agars of the usual nutrient concentration and firmness, no special precaution regarding humidity need be taken except that tube cultures should be stoppered with fairly compact cotton plugs, and that petri dishes should be fairly close fitting. When testing strains of *Penicillium expansum* or *P. italicum* and *P. digitatum* for their capacity to rot pomaceous or citrus fruit respectively, it is advisable to incubate the inoculated fruit in desiccators or other vessels where a humid atmosphere can be maintained if one wishes to secure the maximum and most characteristic development of these fungi on the surface of the rotting fruit.

Preservation of Cultures

Any method of culture preservation, to be successful, should preserve cultural, morphological, and physiological or biochemical characteristics in as nearly unaltered form as possible. For specific strains, methods may need to be altered to accomplish this objective. Particular attention should be given to the perpetuation of cultures which represent species types, and strains which are significant for their biochemical reactions. There should be no question regarding the continuity in culture of particular strains which for one reason or another it is important to maintain. The careful worker may be able to determine whether or not he is working with an organism culturally and morphologically similar to one previously reported; he cannot, however, without actual test, know whether he is dealing with a strain responsible for a desired biochemical reaction. Various methods of culture preservation have been successfully applied to the Penicillia and other molds in our Laboratory over a period of years, and were given rather detailed consideration in Thom and Raper's "Manual of the Aspergilli" (1945). Hence, it should be sufficient to review these only briefly in the present work.

TYPES OF CULTURES

Agar Slants: The method generally employed for maintaining mold cultures, and one which has been successfully used in our laboratories over a period of more than four decades, may be referred to as the "agar slant

method." This involves the periodic transfer of spores from old slant or plate cultures to new agar tubes. For most species, Czapek's solution agar can be used satisfactorily. For perithecial forms it is better to use malt or corn meal agar for reasons already cited (see p. 68). For a few species, such as *Penicillium albicans* Bainier, some medium such as steep agar containing abundant amino nitrogen is desirable. Transfers should be made frequently enough to maintain the viability of the most short-lived species. We have found from our experience that 8 to 9 months represents a safe, and not too tedious, interval. New tubes are inoculated in triplicate. After a proper incubation period the least characteristic culture is discarded. The remaining two cultures are retained for preservation, one being added to our stock collection and the other being held in a reserve collection. Both collections are stored in separate refrigerators at a temperature of 2° to 4°C. (fig. 20). Storage at this temperature materially lengthens the viability of many species. Stock cultures maintained in this way should be periodically recultivated in petri dish cultures and carefully examined to confirm the authenticity and typical character of the individual strains.

Lyophil Preservation: The preservation of molds in lyophil form has been practiced at this Laboratory since 1941 and results obtained up to this time lead us to consider it the most desirable method for preserving cultures of the Penicillia. The techniques employed have been described in detail elsewhere, by Raper and Alexander (1945a) and by Thom and Raper (1945), hence need not be repeated here. It is sufficient to say that the process involves the suspension of conidia in sterile blood serum or some other protein-rich medium. The resulting suspension is distributed into small glass tubes which are attached to a manifold and are then immersed in a freezing bath at a temperature of −40 to −50°C. The suspensions are frozen instantly. Evacuation of the system by means of a vacuum pump protected by a conventional water-trap is initiated and the cultures are completely desiccated from the frozen state. When dry, the tubes are sealed off with a gas-oxygen torch so that each of the individual preparations retains within itself the degree of vacuum present in the system when the seal was made. An apparatus of the type employed is shown in figure 21. Lyophil preparations are stored in a refrigerator, although it is not known that this precaution is necessary. Cultures of many Penicillia preserved in this way (Raper and Alexander, 1945) have been tested for viability at the end of a five year period and, without exception, have been found to retain their cultural and morphological characteristics. Strains preserved in lyophil form appear to retain their physiological and biochemical characteristics. The capacity to produce penicillin was found to remain unaltered in penicillin-producing strains

tested in a series of experiments conducted by Raper and Alexander (1945) over a two-year period. It is our belief that this process possesses certain distinct advantages: (1) there is no possibility of contaminants entering the sealed preparations; (2) the investigator recultivating the molds starts with the spores contained in the original suspension; (3) the space required for storage of lyophil preparations is much less than for any other type of culture (fig. 22).

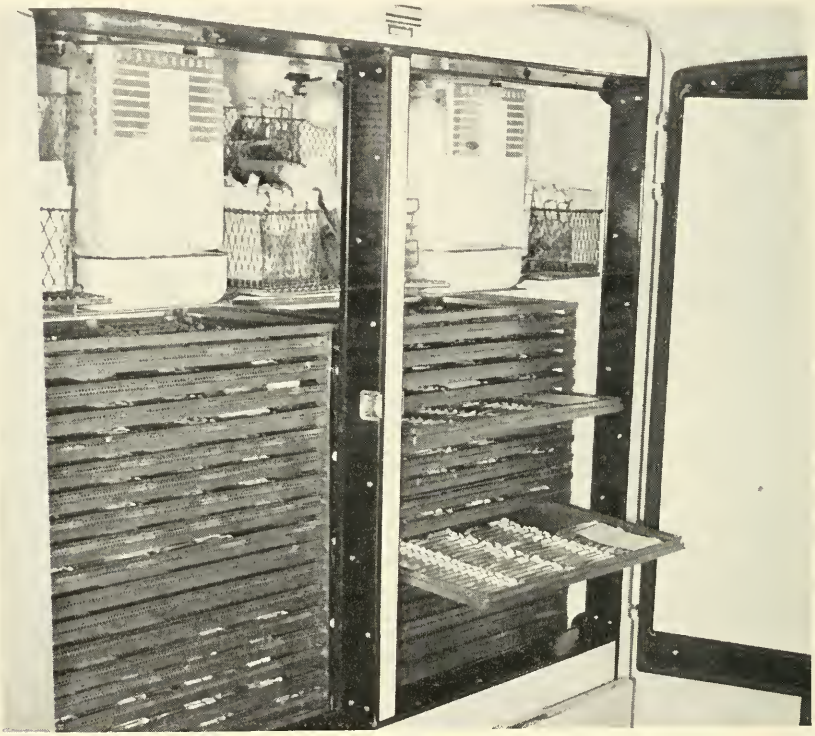


FIG. 20. Refrigerator adapted for storage of stock cultures of Penicillia and other molds. The flat sliding trays are fashioned of perforated brass sheeting to permit free circulation of air.

Soil Cultures: Cultures of Penicillia, like many other microorganisms, can be successfully maintained in soil. The method used in our Laboratory follows that described in 1934 by Greene and Fred at the University of Wisconsin. While this method has not been employed on a scale comparable with the agar slant method, or the lyophil method, it has given satisfactory results wherever used. Preservation in soil offers the advantage that it enables the investigator to remove source material for subcultures from a single stock over a long period of time if proper precautions

for asepsis are exercised. It is known that this method of culture preservation is commonly practiced in the laboratories of penicillin manufacturing industries. Some workers successfully maintain cultures of penicillin producing molds in dry sand or a mixture of sand and talc. In the absence of any colloidal material to serve as a possible protective coating

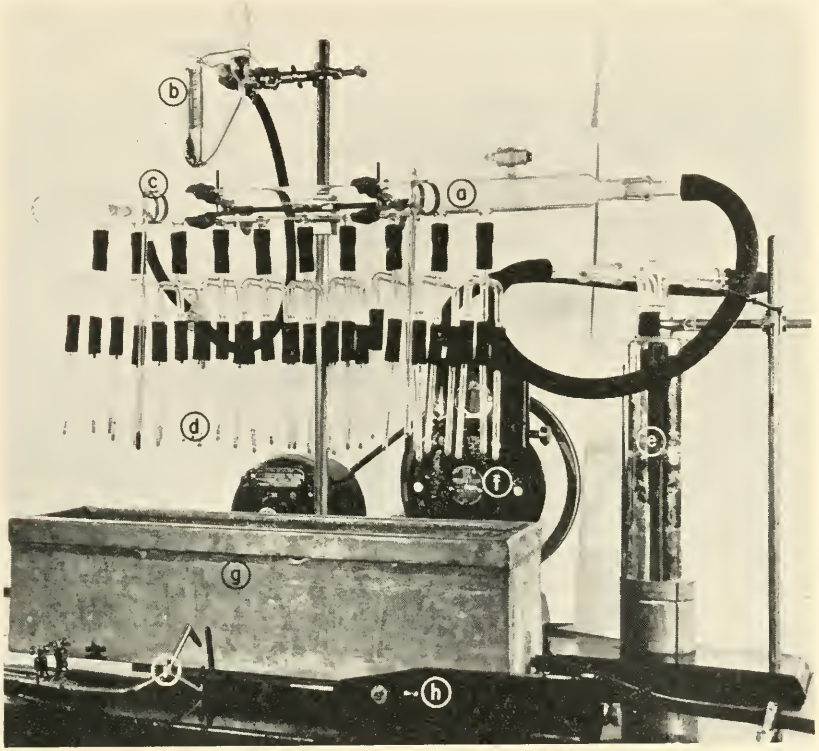


FIG. 21. Lyophil apparatus, table model. *a*, Manifold; *b*, Bruner-type vacuum gauge; *c*, thermometer; *d*, lyophil preparations in final stages of desiccation; *e*, Dewar flask containing a water-vapor trap immersed in CO_2-ice and methyl cellosolve; *f*, vacuum pump; *g*, insulated freezing bath; *h*, vacuum tester; *i*, oxygen-gas torch. (After Raper and Alexander, Mycologia, 37, 1945).

for the spores, it is difficult to see how the sand or talc could exert any favorable effect. Members of the *Penicillium chrysogenum* series are known to be especially long-lived in culture, and it is possible that equally good results might be obtained by preserving a mass of spores in a dry state in the absence of any type of extender.

Preservation under Oil: During recent years several mycologists have adopted a method of culture preservation wherein a strain is permitted to reach a suitable stage of development and is then covered with a layer of

sterile mineral oil, usually extending about 1 cm. above the edge of the agar slant or colony margin. Exact figures on viabilities are not available, but reports have been received covering three to four years. The method is considered to be especially adaptable to the preservation of forms that sporulate very lightly since mycelial elements, as well as propogative cells such as conidia appear to retain their viability. Buell and Weston (1947) discussed this technique and presented favorable results obtained over a two-year period.

FIG. 22. Storage of lyophilized cultures, showing the limited space required. A metal box 12½ inches by 14½ inches will accommodate 306 vials, each containing four desiccated preparations as shown.

LONGEVITY

Species of *Penicillium* vary materially in their ability to remain viable in laboratory cultures. Some series survive for several years when stored as dry agar slants; others die off fairly rapidly. Some series of transfers have been made to reach a basis for generalization but the factors involved are too numerous to justify generalization. In our experience, members of the *Penicillium chrysogenum* series have been found to be especially long-lived. Of a total of 42 strains belonging to this series, which were brought to the Northern Laboratory in 1940, all but three were found to be viable in agar slant tubes when tested five years later. It is inter-

esting to note that during this time these old stocks had been stored for a considerable period in a room where the temperature commonly reached 35 to 40°C. during the summer months. In no other series was a comparable longevity encountered. Scattered ascosporic strains in the *P. javanicum*, *Carpenteles*, and *P. luteum* series yielded viable cultures, as did also occasional members of the *P. rugulosum* and *P. purpurogenum* series. In many of the better known series represented by such species as *P. roqueforti*, *P. stoloniferum*, and *P. nigricans* all of the strains were dead. Strains of *Paecilomyces*, like members of the *P. chrysogenum* series, represented an exception with the majority of strains remaining viable after five years. In contrast to the long-lived forms, some species of *Penicillium*, such as *P. italicum* and *P. digitatum*, usually lose their viability in less than a year unless they are stored at refrigerator temperatures.

DEGENERATION

Our Collection of Penicillia, upon which the current study is largely based, contains strains of a number of species isolated in 1904. Other forms go back from 30 to 40 years in continuous culture. Some strictly conidial strains, such as *Penicillium roqueforti* (NRRL 849) and *P. camemberti* (NRRL 877) have remained unchanged when transferred with rigorous care. Other conidial forms handled with equal care have shown progressive variation and degeneration in culture. Thom's type of *P. oxalicum* (NRRL 787), which originally represented a strictly velvety and heavily sporing strain, now produces rather floccose and lightly sporulating colonies quite unlike the original. *Penicillium purpurogenum* var. *rubri-sclerotium*, when first isolated, produced sclerotia and abundant typical biverticillately symmetrical penicilli in culture. Sclerotium production has been lost completely and today this strain produces colonies atypical in pattern and texture which sporulate lightly upon all substrata In both of these strains, however, cellular elements of the penicilli remain characteristic of the species and there can be no question of continuity in culture from the original strain.

Loss of ascospore production represents a common occurrence in strains characterized by abundant perithecia and ascospores when first isolated. This has sometimes been attributed to the gradual elimination from such a culture of one of the haplonts necessary for development of the perfect stage. Emmons (1935), however, showed that all of the species of *Penicillium* studied by him were homothallic and capable of developing colonies with typical perithecia when started from either individual conidia or ascospores. Loss of the ascosporic stage must, therefore, be sought in some other source, possibly nutritional in character.

Parasitization

Some species of *Penicillium* parasitize the mycelia and fruiting structures of *Aspergillus* species and other saprophytic molds. *Penicillium*

Fig. 23. *Penicillium* sp. parasitic on *Aspergillus niger*, × 165. (Photograph by Edward Yuill, Manual of The Aspergilli, Williams & Wilkins, 1945).

rugulosum Thom and *P. purpurogenum* Stoll in particular, are able to infect, overgrow, and destroy cultures of *Aspergillus niger*, *A. tamarii* and *A. flavus*. When such infections occur in fermentation processes, yields of acid or other products may be greatly reduced. Cases of parasitism between a *Penicillium* and a black *Aspergillus* are easy to demonstrate (fig. 23). Other cases of intimate mixture or parasitism may be difficult

to recognize, hence the importance of exercising the greatest possible care in the making of every transfer cannot be over emphasized.

Contamination

In routine laboratory work, strains of *Penicillium* may become contaminated with bacteria, yeasts, and actinomycetes unless proper safeguards are exercised. Such contaminated cultures may go unnoticed for considerable periods of time if the substratum employed does not particularly favor the growth of the contaminant. Cultures can be readily repurified as a rule by the techniques described under dilution and streak cultures.

Detection of contamination by actinomycetes may be unusually difficult, since a few species of *Penicillium* themselves produce an odor strikingly like, or identical with, that produced by many actinomycetes. *Penicillium biforme* Thom is a case in point. Over a period of many years Thom unsuccessfully attempted to demonstrate the presence of an actinomycete which could account for its characteristic earthy odor. Westling and Biourge reported similar experiences. In this case it has been shown beyond reasonable doubt that no foreign organism is present. In other cases the development of similar odors undoubtedly results directly from such contamination. The worker handling cultures of *Penicillium* must, therefore, exercise every possible precaution and must in certain cases repeatedly confirm the purity of his cultures.

Cultures of *Penicillium* may become contaminated by molds of other genera. Westling's culture of *Penicillium baculatum*, as received by Thom, was found to contain a culture of *Aspergillus repens*, and it is believed probable that the ascosporic stage which Westling (1910) described for *P. baculatum* was based upon this *Aspergillus*.

Hygiene

The Penicillia are characterized by the production of tremendous numbers of aerial spores or conidia, which are very small and very light. They are carried about by the slightest air currents, hence tubes or plates containing mature colonies should be open for the minimum time necessary to effect reinoculations, and rough handling should be avoided always. Every possible precaution should be taken to work in an area where the air is entirely quiescent. When large numbers of transfers are to be made, a special inoculating room or culture chamber should be available, and it is desirable that the walls should be finished in some material which can be sponged with antiseptics or steamed out from time to time. Air entering the room should be sterile (a convenient means of obtaining sterile air is to force incoming air through appropriate paper or cloth filters that

are manufactured for this purpose). All discarded cultures should be killed by heat.

Mites

Mites are brought into every laboratory engaged in the study of the flora of raw products such as soil, cheese, mildewed textiles, etc. Rigid isolation of the raw material brought in, with constant cleaning of the working space, tools, and the hands of the worker, are the necessary price for preserving purity in the cultures handled. Mites travel slowly, but they keep going. They migrate from petri dish to petri dish through a whole incubator and leave eggs, bacteria, and miscellaneous spores picked up en route. They can go through cotton plugs, provided the culture within attracts them, for they seem to avoid some species and destroy all of other series. Some mites are so small as to escape notice by the naked eye, others are easily seen. The presence of mites can usually be detected by a characteristic odor in the infected cultures.

Elimination of mites by sanitary measures is possible when rigorous control measures are exercised. Stock cultures should be protected against a possible invasion by mites. A satisfactory protective measure consists in moistening the cotton plugs with the following solution:

95 per cent alcohol	95 ml.
Biehloride of mercury	0.5 gm.
Glycerine	5 ml.
Color with any of the aniline dyes	

The cultures must be allowed to develop into typical colonies before poisoning and care must be taken that the solution does not come in contact with the colony. An antiseptic formula for the purpose needs alcohol to insure penetration of the plug, a poison to destroy the mites, glycerine to prevent the crystallization of the poison as the alcohol evaporates, and a dye to insure the destruction of the cotton plugs when removed from the tubes. The above treatment of cotton plugs likewise protects cultures from invasion by certain molds which grow at low temperatures and might otherwise grow through the cotton.

Table tops and other exposed surfaces may be successfully freed of mites by washing with an alcoholic solution saturated with paradichlorobenzene and containing two to five parts of glycerine. Kerosene and other selected petroleum fractions may likewise be used for this purpose. They may also be used in the form of a fine mist to decontaminate incubators should these become infested.

The same precautionary and control measures may be employed against roaches and other small insects which often inhabit laboratories and sometimes infest plate cultures.

Preservation of Species Types

DRIED SPECIMENS

In general botanical taxonomy the description of a species should apply to a particular specimen marked as type and deposited in some accessible collection for reference. In the case of *Penicillium*, earlier workers have commonly deposited such type specimens in herbaria. Oftentimes these consisted of natural specimens such as rotted fruit. In some cases they represented colonies grown by conventional means but transferred and dried on sheets of cardboard; in other cases they consisted of portions of colonies mounted inside paper boxes designed to protect aerial parts; in still other cases cultures dried in original tubes or petri dishes have been preserved. Specimens of the latter type generally offer the most satisfactory material, since they retain the original colony characters in least altered form. The preservation of such dried specimens, while highly desirable, gives only limited satisfaction. When cultures of *Penicillium* become thoroughly dry the mycelium and fructifications of most species are exceedingly fragile and usually break up completely when attempts are made to prepare microscopic mounts. In many cases the form and dimensions of conidia represent the only points which can be established with any degree of certainty and even here errors may occur as a result of drying to give a shriveled appearance.

LIVING COLLECTIONS

The preservation of living type material, if handled with scrupulous care, affords the best solution in the case of most Penicillia. For this reason collections of *Penicillium* and other saprophytic molds have gradually been built up. If such collections, however, are not expertly handled the strains contained in them may not only fail to represent the original types but may, in fact, be very misleading in giving the worker a false sense of security. The existence of certain species which tend to degenerate under continuous laboratory cultivation represents the most serious objection to this method of preserving type material.

Bainier, in Paris, maintained a fairly large collection until his death. This was subsequently taken over by other workers and what remained of it in 1922 was sent to Thom by daFonseca. Westling's cultures had been previously received in 1911. Biourge inherited the collection left by Dierckx and augmented it greatly by the isolation of additional strains in Europe. His collection was sent to Thom prior to the publication of the latter's Monograph in 1930. Some additional cultures from Biourge's collection were brought to this country in 1936 by Professor Paul Simonart who succeeded Biourge at the University of Louvain. In 1940, the collec-

tion formerly maintained by Thom, Thom and Church, and Thom and Raper, was moved to the Northern Regional Research Laboratory where it formed the nucleus of the Collection developed here. Since that time many additional cultures have been added through isolations made at this Laboratory and through the receipt of cultures from collaborators throughout the United States and abroad. An unusually large number of strains was contributed by Professors W. H. Weston, G. W. Martin, and W. G. Hutchinson, and W. Lawrence White in connection with the study of deterioration of military equipment during World War II.

Other valuable and noteworthy collections of Penicillia are maintained at the Centraalbureau voor Schimmelcultures, Baarn, Holland by Professor Westerdijk and her staff, and at the London School of Hygiene and Tropical Medicine by Mr. George Smith in connection with the biochemical studies of Professor Harold Raistrick and co-workers. Over a period of many years we have enjoyed the full cooperation of Professor Westerdijk's laboratory. All of Zaleski's types were sent to Thom in 1928. For the present study a total of almost 300 cultures of *Penicillium* and related forms were supplied and have been included in our comparative studies. A free exchange of cultures has likewise been maintained between our Collection and that of Professor Raistrick and George Smith.

We have attempted to include in the present study the most extensive and representative group of Penicillia that it was possible to assemble.

Cultures discussed in this Manual are maintained as agar slant cultures in our Collection, and have been preserved in lyophil form. It is hoped that this method of preservation, in particular, will keep available for other investigators cultural material truly representative of our species concepts. Selected strains representative of the species recognized in this Manual have been deposited with the American Type Culture Collection, Washington, D. C.; the Centraalbureau at Baarn; and the London School of Hygiene and Tropical Medicine.

Chapter V

PENICILLIN

Penicillin was discovered by Professor Alexander Fleming in 1928. He observed that colonies of *Staphylococcus* surrounding a contaminating blue-green mold failed to grow. Fleming isolated the mold in pure culture; demonstrated its capacity to produce a powerful bacteriostatic substance, which he named "penicillin"; and recommended the use of the substance for obtaining pure cultures of *Bacillus influenzae* (1929). He noted in addition that it might have therapeutic value if it could be produced in quantity, for he found it to be highly effective against a number of Gram-positive bacteria when tested in laboratory cultures. In 1932 Clutterbuck, Lovell, and Raistrick published the results of their limited studies on the production of penicillin by Fleming's mold. In this country, Roger Reid (1933, 1934, 1935) confirmed the production of an antibacterial substance by the same mold, but did not isolate the antibiotic or add materially to the information already published by Fleming and Raistrick's group in England.

Interest in penicillin was revived in 1940 through the demonstration of its potential therapeutic value by Professor H. W. Florey, E. Chain, and others at Oxford University. The following year the same group published a more detailed account (Abraham, *et al.*) in which methods of production and assay were described, and in which some clinical trials were reported. Shortly before this the work on penicillin at Oxford had been interrupted due to war conditions, and Professor Florey and Dr. N. G. Heatley had come to the Northern Regional Research Laboratory where work on penicillin was initiated in July 1941. Here a broad program of research was undertaken (1) to develop a more productive culture medium, (2) to find molds capable of producing increased yields of penicillin, and (3) to develop, if possible, methods for the production of penicillin in submerged culture.

Early developments in this country have been reported by Coghill (1944), Thom (1945), and Raper (1947), whereas the story as it unfolded in England has been told by Fleming (1944), Chain and Florey (1944), and others; it need not be repeated here. Popular accounts have been published by Ratcliff (1945) and Masters (1946).

Surface Production and the Development of a Suitable Medium

Early studies at the Northern Laboratory centered around the production of the antibiotic in surface culture (fig. 24A), the method which had

been used by Fleming and by the Oxford group. Particular attention was given to the development of an optimum medium for penicillin production, and the successful and highly significant results of this work have been published by Moyer and Coghill (1946a). The most important constituent of the optimal medium was corn steep liquor, which, at levels below actual toxicity, was found to produce yields of penicillin more or less proportional to the amount of steep liquor contained in the medium. Of various carbon sources tested, lactose was found to give the highest penicillin yields, and afterward was regularly included in the production medium. The lactose-steep liquor medium, thus evolved, was generally adopted for the commercial production of penicillin by surface culture methods (see p. 000). Studies of a similar but less productive nature were reported by Foster, *et al.* (1943).

Much attention has been given to the use of other ingredients without finding, up to this time, any substitute equal to the lactose-steep liquor combination. Foster, *et al.* (1946) have recommended the use of cotton-seed meal as a substitute for corn steep liquor. Mohan, *et al.* (1946) reported bran extract to favorably influence penicillin production. Cook, *et al.* (1945) reported the successful use of extracts of ground peas (*Pisum sativum*). Taylor (1943) used "amigen," a partially hydrolyzed starch preparation, as a carbon source. Lochhead and Chase (1945) used sulphite waste liquor as a basal substrate, obtaining increased yields when they supplemented this with additional inorganic nitrogen and phosphorus, or corn steep liquor. Shwartzman (1944) claimed enhanced production of penicillin in fluid media containing cellophane. Murkherjee and Sarkhel (1946) reported glycerine to afford a suitable carbon source.

Bowden and Peterson (1946) investigated a number of natural materials but found no satisfactory substitute for corn steep liquor, although they obtained increased yields of penicillin by supplementing the corn steep liquor with meat-scraps meal and potatoes. They likewise reported that prior fermentation of the corn steep liquor with yeast seemed to increase penicillin production. Knight and Frazier (1945) investigated the effect of corn steep liquor ash on penicillin production and obtained some increase by the addition of such ash to the usual production medium.

Miscellaneous Production Methods

Various methods of producing penicillin have been investigated. The production in surface or still cultures was first investigated, and was practiced on a commercial scale for a period of two to three years prior to 1945. Clifton (1943) proposed trickling the culture medium through a column of wood shavings, of the type used in vinegar manufacture, which had been inoculated with a favorable mold strain. Various investigators studied the

production of penicillin upon bran, employing techniques similar to that used for the production of diastatic enzyme preparations with *Aspergillus oryzae*. Before penicillin as a drug became generally available, several investigators (Hobson, 1944; Alston, 1944; and Dunayer *et al.*, 1944) studied the production of "crude penicillin," usually by growing the mold on sterile gauze saturated with a suitable culture solution and subsequently applying such gauze preparations directly to surface wounds. By this method, patients for whom penicillin would otherwise have been unavailable were

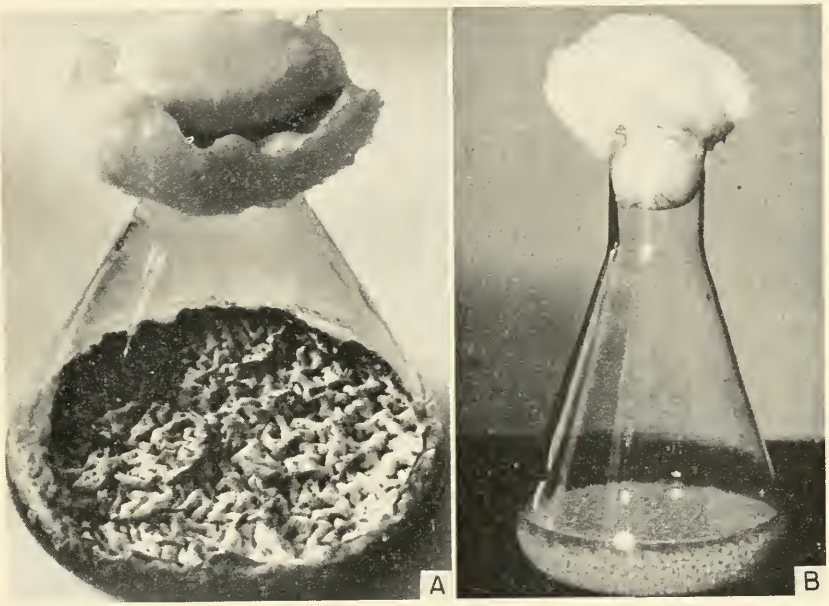


FIG. 24. Laboratory methods of producing penicillin. *A*, Surface or still culture of *Penicillium notatum*, NRRL 1249.B21, in a wide bottom Fernbach flask (2.8 liters). *B*, Submerged or deep culture of *P. chrysogenum*, NRRL 1951.B25, in a 300 ml. Erlenmeyer flask.

treated with the drug. Carpenter, *et al.* (1945) produced such preparations in considerable numbers for use in the Hawaiian Islands and by the Navy in the South Pacific area (see also Agmar, 1945; and Larsen, 1945). Certain dangers inherent in this practice in the absence of rigorous asepsis, were pointed out by Raper and Coghill (1943).

SUBMERGED PRODUCTION

Of the various methods proposed, the production of penicillin in submerged culture was early realized to be the most important (fig. 24B), and particular attention was given to the development of this type of fermenta-

tion at the Northern Laboratory and elsewhere. The successful results of studies conducted here were reported by Moyer and Coghill (1946b), while more or less similar investigations were reported by Foster, Woodruff, and McDaniel (1946). In the former studies it was found that the same type of nutrient solution used for surface production of penicillin, could be employed, but that the concentrations of lactose and of corn steep liquor should be reduced approximately one-half. The formulas of media developed by Moyer for surface and submerged production of penicillin, and reported in papers by Moyer and Coghill (1946a and 1946b), follow:

	Surface production	Submerged production
Corn steep liquor	100.0 g.	40.0 g.
Lactose	44.0 g.	27.5 g.
$NaNO_3$	3.0 g.	3.0 g.
KH_2PO_4	0.500 g.	0.500 g.
$MgSO_4 \cdot 7H_2O$	0.250 g.	0.250 g.
$ZnSO_4 \cdot 7H_2O$	0.044 g.	0.020 g.
Glucose	2.75 g.	3.00 g.
Water to make	1 liter	1 liter

Sterilize in autoclave for 20 minutes at 15 lb. pressure and 120°C.

To the solution for submerged culture, sterile calcium carbonate was usually added in the amount of approximately 1 per cent just prior to inoculation.

Starting with the basic information developed at the Northern Laboratory, Professors Peterson and Johnson and their associates at the University of Wisconsin have investigated in great detail the various factors affecting the production of penicillin in submerged culture, both in the laboratory and on a semi-plant scale (fig. 25). While a detailed analysis of their content is not necessary in this connection, the following papers should be cited: Knight and Frazier, 1945 a and b; Koffler *et al.*, 1945, 1946, 1947; Johnson, 1946; Gailey, *et al.*, 1946; Stefaniak, *et al.*, 1946a and 1946b; and Peterson, 1947. In general, the levels of nutrients, aeration, pH, etc., cited in these papers are believed to approximate those employed for large scale production by industry.

In laboratory experiments, cultures are usually seeded with conidia, or a suspension of conidia, derived directly from heavily sporing cultures as reported by Moyer and Coghill (1946a), and others. Under some conditions the production of seed material in submerged culture has marked advantages. Foster, *et al.*, (1945) reported methods of obtaining heavy conidium production under these conditions and reported a high concentration of the calcium ion to be the most important factor involved. Gilbert and Hickey (1946) found the addition of iron in fairly high concentrations to stimulate submerged sporulation. Savage and Vanderbrook (1946) demonstrated that mycelium fragmented in a high speed blender provided suitable seed for setting penicillin fermentations.

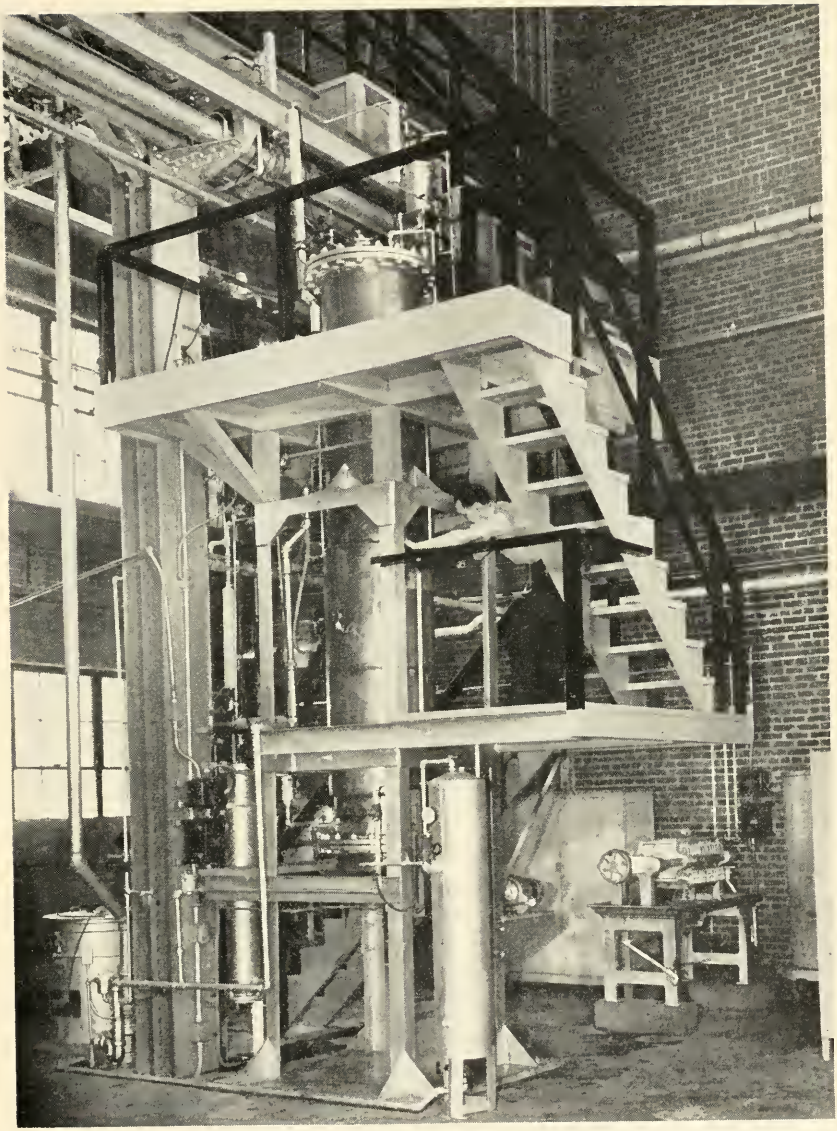


FIG. 25. Stainless steel vat fermenter of 150 gallon capacity employed at the Northern Regional Research Laboratory for pilot plant studies in penicillin production and other fermentations.

White, *et al.* (1945) reported the development of a synthetic medium for penicillin production and obtained yields up to 80 or 90 per cent of those produced on the usual lactose-steep liquor medium. Amino acids in the

corn steep liquor appeared to be largely responsible for its activity. Stone and Farrell (1946) developed a synthetic medium suitable for penicillin production, but it has not been generally adopted since yields do not exceed those obtained in media containing corn steep liquor and the substratum is somewhat more expensive. Cook and Brown (1946) have also proposed a synthetic medium based upon their prior studies of *Pisum* extracts. Pratt and co-workers (1945 and 1946) investigated the influence of inorganic salts on the penicillin fermentation.

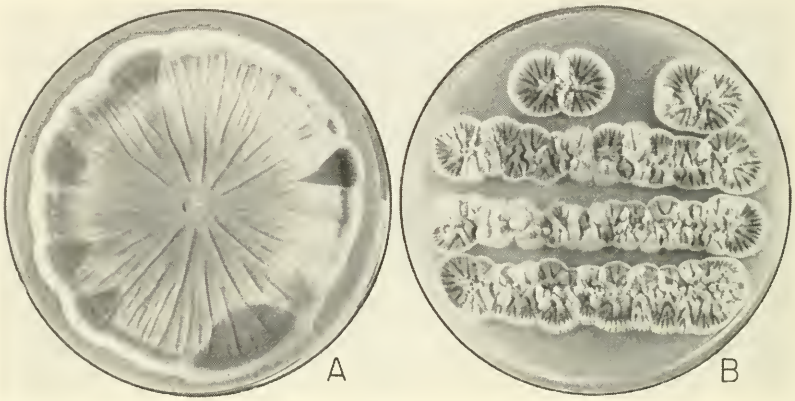


FIG. 26. Cultures of penicillin-producing molds from which variant substrains may be isolated. *A*, Three-week-old colony of *Penicillium notatum*, NRRL 1249.-B21, on steep agar showing conspicuous sectors; *B*, Streak culture seeded with mycelia (in pellet form) from a one-week-old submerged culture of *P. chrysogenum*, NRRL 1951.B25. (After Raper and Alexander, Jour. of The Elisha Mitchell Scientific Society, *61*, 1945.)

DEVELOPMENT OF MORE PRODUCTIVE STRAINS

Much study has been devoted to the development of improved penicillin producing organisms. All of the early work, both in England and the United States, was conducted with Fleming's original strain of *Penicillium notatum*. It was early discovered at our Laboratory and elsewhere that this mold was subject to considerable variation in culture (fig. 26A). Subcultures showing definite cultural characteristics were isolated and tested for penicillin production, and a limited number of monospore selections were made. One of these, designated NRRL 1249.B21 (fig. 27C), was found to produce greatly increased yields in surface culture and was widely used for the commercial production of penicillin by this method (see Moyer and Coghill, 1946a and Raper and Alexander, 1945b). Attempts to further increase yields of penicillin by continued strain selection proved ineffective although a wide range of natural variants (fig. 27) were isolated and tested (Raper and Alexander, 1945b).

After it was found that penicillin could be produced in submerged cul-

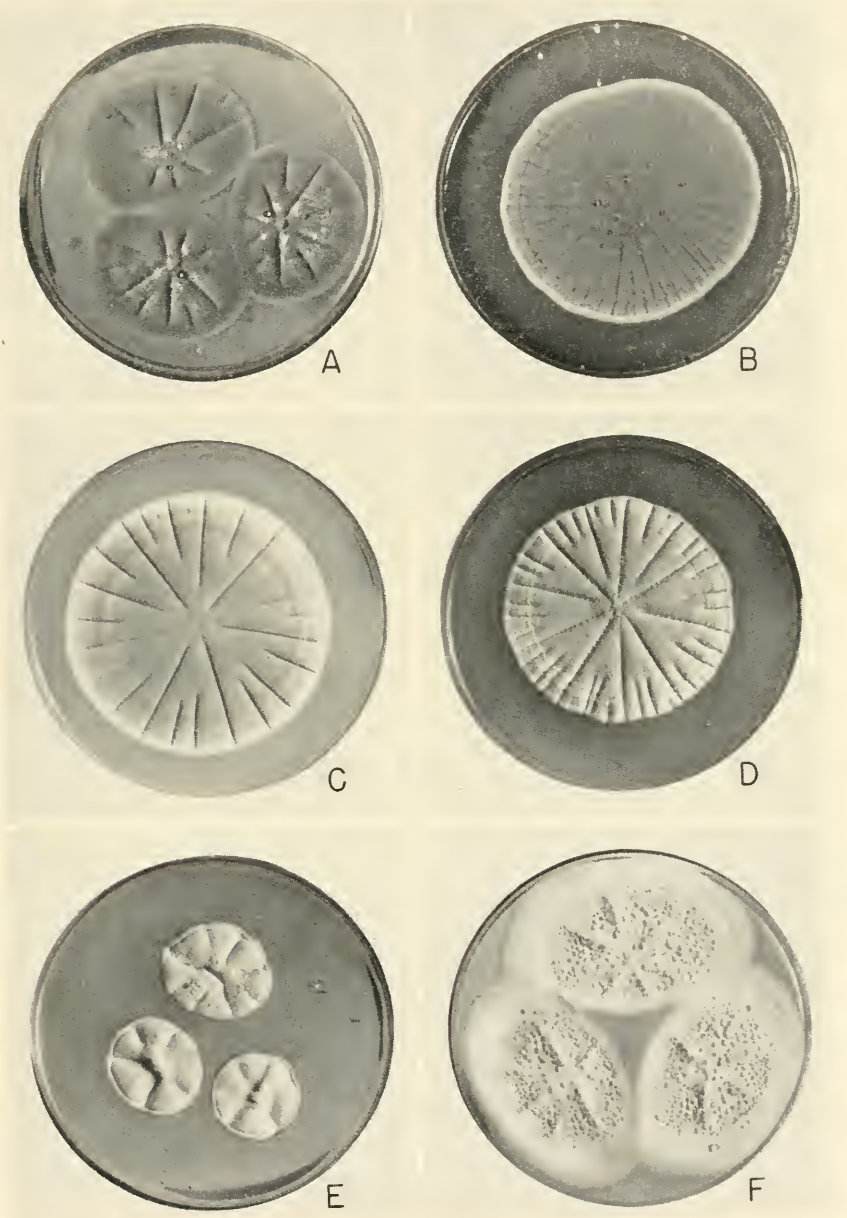


FIG. 27. The Fleming culture and selected derivative strains. *A*, Stock, the Fleming culture, NRRL 824. *B*, The Squibb strain derived from it, NRRL 1249. *C*, NRRL 1249.B21, the strain most widely used for penicillin production in surface culture. *D*, *E*, and *F*, Substrains of 1249.B21 showing varying patterns of growth and a progressive reduction in spore production. (After Raper and Alexander, Jour. of The Elisha Mitchell Scientific Society, *61*, 1945.)

ture, and that this method of production was the most feasible industrially, particular attention was directed toward the development of strains capable of producing greater yields under these conditions. A strain of *Penicillium notatum*, NRRL 832 (fig. 97E), was the culture first found to produce satisfactory yields when grown submerged. Attempts to develop higher yielding substrains from it were unsuccessful (Raper and Alexander, 1945b). A wide search for other and possibly higher yielding strains was, therefore, undertaken. A simple screening technique (fig. 28) was developed which quickly and effectively eliminated poor producing strains, whereas more promising strains were tested in flask cultures. Of many cultures isolated

FIG. 28. Screening test for preliminary evaluation of penicillin producing molds. *A*, The selected mold is grown upon steep agar at 24°C., and a radial series of agar plugs removed with a cork borer at 4 (upper), 6 (lower), and 8 (center) days. *B*, The agar plugs are placed upon an agar plate, previously seeded with *Staphylococcus*, and incubated for 16 hours at 37°C. Resulting zones of inhibition are compared with zones produced by controls representing known good penicillin producing strains grown and tested under identical conditions.

and examined by Raper, Alexander, and Coghill (1944) a strain of *P. chrysogenum*, NRRL 1951, (isolated from a cantaloupe in Peoria), proved to be the most productive (Col. Pl. II and fig. 95). Selective recultivation of naturally occurring variant types from this strain soon yielded a substrain, NRRL 1951. B25 (Col. Pl. II and fig. 29), which produced penicillin yields up to 200–250u/ml. in submerged culture. Attempts to realize further increases in yield by the isolation and testing of natural variants of NRRL 1951.B25 were unsuccessful, although even a wider range of variants was obtained (fig. 30) than had been encountered in NRRL 1249.B21 (Raper and Alexander, 1945b).

Under a program of research sponsored by the Office of Production Research and Development, conidia of strain NRRL 1951.B25 were subse-

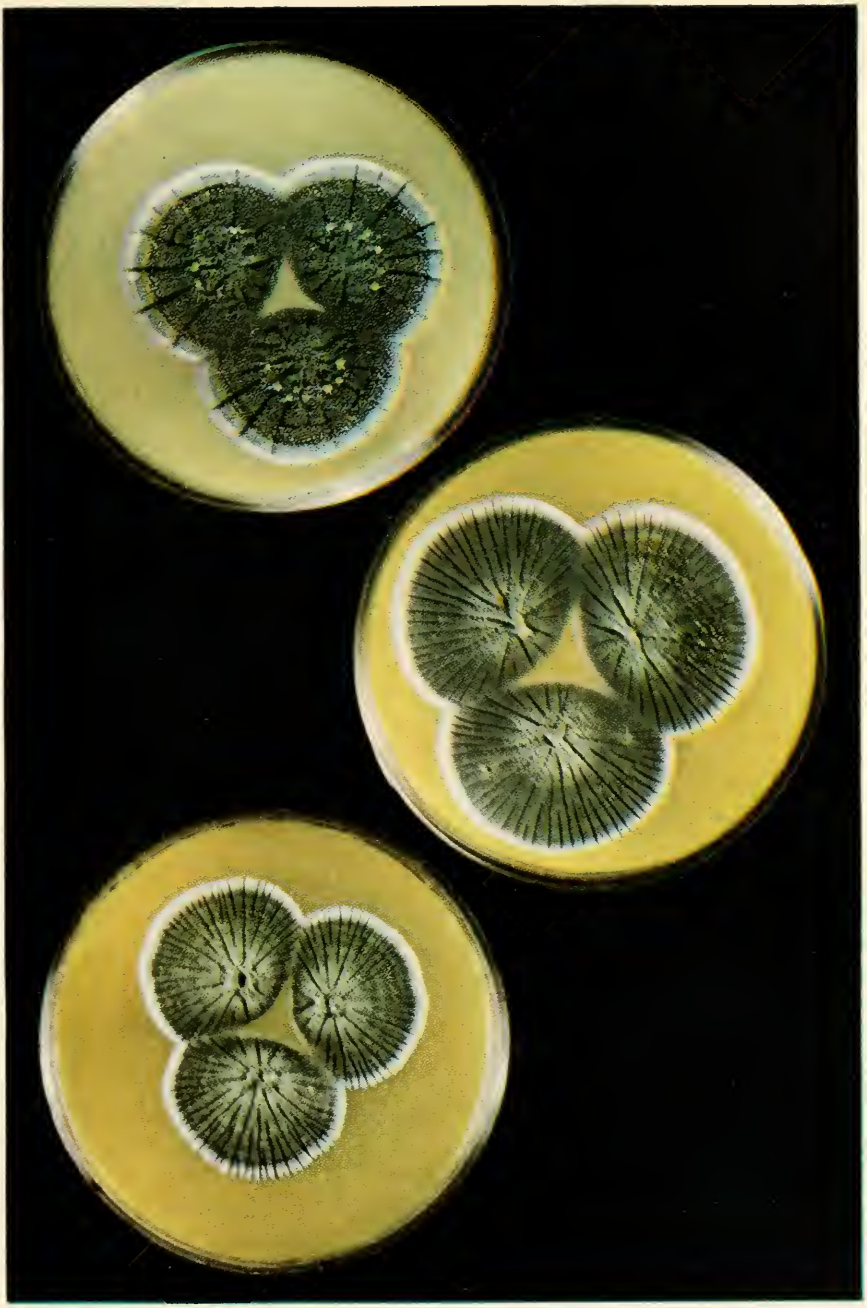


PLATE II

Development of improved penicillin-producing strains in a selected culture of *Penicillium chrysogenum* Thom
TOP: Parent strain, NRRL 1951, isolated from a cantaloupe at the Northern Regional Research Laboratory which yields penicillin up to 100u/ml. in submerged culture. *CENTER:* A natural variant, NRRL 1951.B25, selected at the same Laboratory which yields up to 250u/ml. *BOTTOM:* An X-ray induced mutation, X-1612, capable of yielding up to 500u/ml.; produced at the Carnegie Institution in Cold Spring Harbor by irradiating conidia of NRRL 1951. B25.
Cultures on steep agar at 12 days. See discussion, p. 96. (Color photographs by Haines, Northern Regional Research Laboratory. Reproduced through co-operation of Chas. Pfizer & Co., Inc.)

quently subjected to X-ray irradiation at the Carnegie Institution in Cold Spring Harbor by Dr. Demerec and co-workers and an induced mutation, designated X-1612 (Col. Pl. II), was developed which produced yields of penicillin up to 500 u/ml. when tested in 80 gallon fermenters at the Uni-

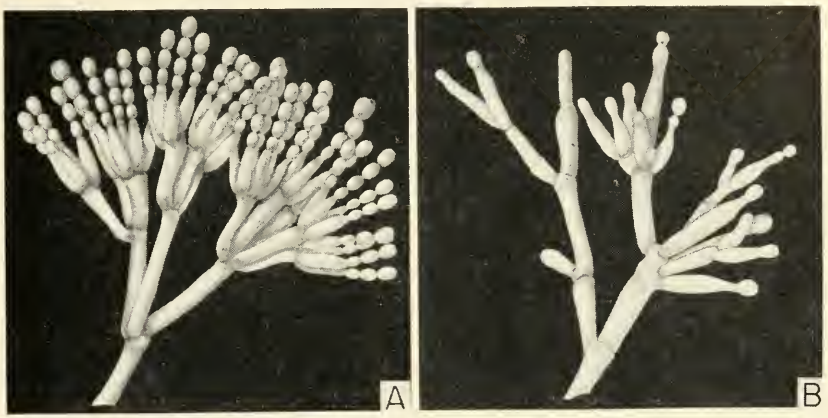


FIG. 29. *A*, Typical penicillus of *Penicillium chrysogenum*, NRRL 1951. *B*, Characteristic penicillus of natural variant, NRRL 1951.B25. Note the irregularity in the arrangement, form, and size of parts in the latter structure, × 750. (After Raper and Alexander, Jour. of The Elisha Mitchell Scientific Society, *61*, 1945.)

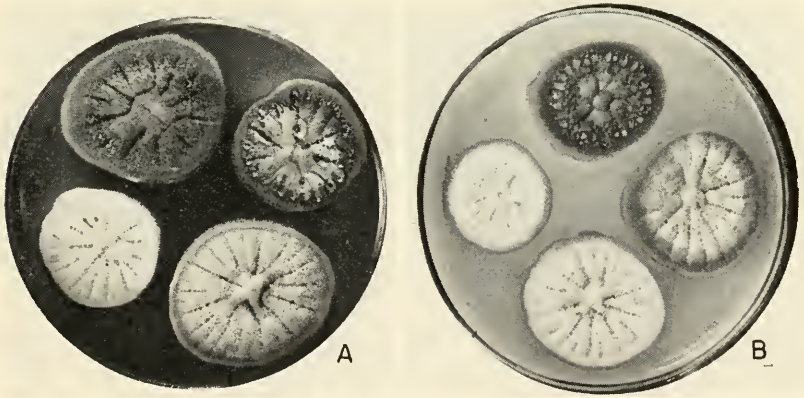


FIG. 30. Variant substrains of *Penicillium chrysogenum*, NRRL 1951.B25, isolated from week-old shaken-flask cultures in penicillin production studies. See fig. 26B.

versity of Wisconsin by Johnson *et al.* (1946). Finally, conidia of strain X-1612 were irradiated with ultra-violet at Wisconsin and a mutation, designated Q-176, was developed by Backus, Stauffer, and Johnson (1946) which produced yields up to 900 to 1000 u/ml. As each of these higher yielding strains appeared, they were quickly adopted by penicillin manu-

facturers. Strain Q-176, or modifications of it which have been subsequently produced in individual laboratories, is still generally used for the commercial production of penicillin.

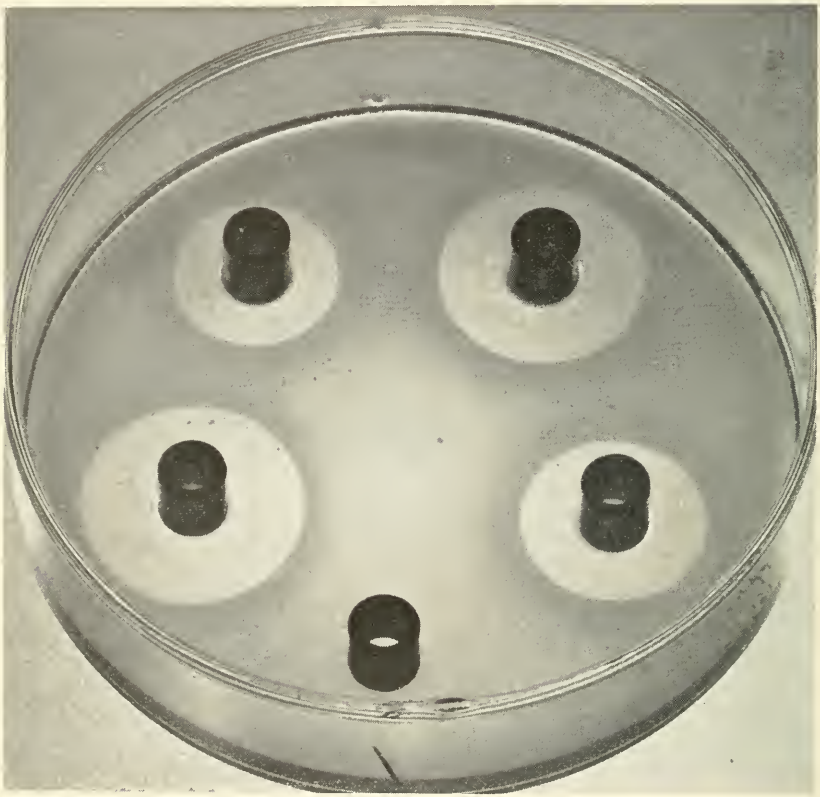


FIG. 31. Cup method of assaying penicillin titres. The cups are placed on the surface of an agar plate heavily and uniformly seeded with *Staphylococcus*, they are then filled with samples to be tested, and the plates are incubated for 16 hours at 37°C. The diameters of the resulting zones of inhibition are a function of the amount of penicillin present. (After Schmidt and Moyer, 1944.)

MICROBIOLOGICAL ASSAY

The method of assaying penicillin first developed by Heatley in 1941, has been generally followed (fig. 31) with certain modifications. Improvements upon the original methods have been reported by Foster (1943a and 1943b), Schmidt and Moyer (1944), Schmidt (1945–1946), Hunter and Randall (1944), and others. Outstanding among such improvements has been the adoption of filter paper discs in place of the porcelain, glass, or metal cylinders formerly employed (Vincent and Vincent, 1944 and Loo

et al., 1945). In addition to the cup assay method, penicillin titres can be determined by serial dilution techniques, or by turbidimetric methods (Joslyn, 1944; McMahan, 1944; and Trussell *et al.*, 1947). Detailed information regarding the different techniques is contained in the papers cited.

Types of Penicillin

Cultures of *Penicillium notatum* and *P. chrysogenum* commonly produce two or more of four types of penicillin, which are generally referred to in this country as F, G, X, and K and in Great Britain as I, II, III, and IV, respectively (Benedict and Langlykke, 1947). Of these, penicillin F was the first to be crystallized. Penicillin G, however, is more stable and is generally produced in much greater amount. This type has gradually come to represent the penicillin of commerce, which is today generally marketed as crystalline penicillin G. Penicillin K shows a greater activity against many organisms in culture than penicillin G, but is chemically less stable and is rapidly eliminated from, or destroyed in, the animal body. It is of comparatively little value therapeutically (Eagle, 1946, 1947a, 1947b, 1947c, and Eagle and Musselman, 1946). The higher yielding strains of penicillin-producing molds, such as X-1612 and Q-176, tend to produce substantial amounts of penicillin K unless measures are taken to prevent such development. It has been found that the addition of phenylacetic acid or phenylacetamide, or some other suitable adjuvant, to the culture solution will markedly reduce the amount of penicillin K and enhance the production of penicillin G (Higuchi *et al.*, 1946). Phenylacetic acid as a constituent of the culture medium was first investigated by Moyer and Coghill (1946c) as a possible means of increasing the total yield of penicillin. Today it performs a much more important function in altering the ratio of penicillins produced by the highest yielding strains.

Penicillin X, or chloroform insoluble penicillin, has a relatively low activity against some test bacteria in agar plates but is retained in the animal body longer than the other penicillins, hence, upon a unit basis represents a more effective drug. In addition, some evidence has been published (Welch, *et al.*, 1944; Ory, *et al.*, 1945; Flippin, *et al.*, 1945; Libby and Holmberg, 1945) which indicates that penicillin X may combat infections that have become resistant to the more common penicillin G. For this reason it appeared desirable to find, or develop, some strain capable of producing high yields of this penicillin in submerged culture. This was accomplished by irradiating with ultra-violet light (fig. 32) a culture of *Penicillium chrysogenum*, NRRL 1984, that had previously been found to be a good "submerged" strain, and producing from it a biochemical mutation, designated NRRL 1984.N22, which formed penicillin X in 50 per cent yield

(Raper and Fennell, 1946). Penicillin X is of particular interest from a chemical standpoint.

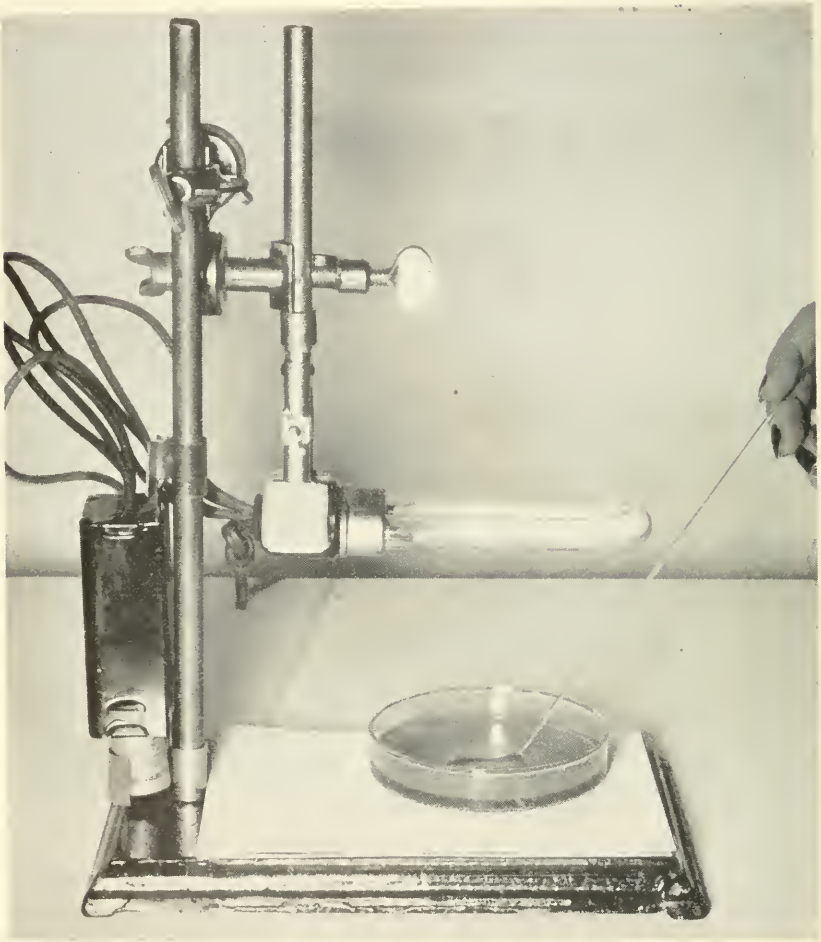


FIG. 32. Simple and effective apparatus and technique used for ultraviolet irradiation of *Penicillium* spores. (After Raper and Fennell, Jour. Bact. *47*, 1946.)

CHEMISTRY

The chemistry of penicillin has been very thoroughly investigated by numerous chemists in university, government, and industrial laboratories collaborating under the joint supervision of the Committee on Medical Research (OSRD, Washington, D. C.) and the Medical Research Council (London). The intense interest was engendered primarily by the belief, held during the early days of commercial production, that the enormous

military needs could be met only if laboratory synthesis were accomplished. A practical synthesis of penicillin has, however, not yet been realized, although a synthesis has been reported by duVigneaud, *et al.* (1946). Fortunately, the production by fermentation processes proved adequate for all war needs.

So far, six naturally occurring penicillins have been isolated in the pure state and all have the empirical chemical formula $C_9H_{11}O_4SN_2R$. The significant penicillin activity is resident in the $C_9H_{11}O_4SN_2$ grouping and all of the penicillins show the same qualitative action against microorganisms. The quantitative differences in potency (from 900–2300 units per mg.) between the penicillins are dependent on the nature of the R group. In penicillin F, R is Δ 2-pentenyl; in Dihydropenicillin F (produced by *Aspergillus giganteus*), R is N-amyl; in flavicidin (produced by *A. flavus*), R is Δ 3-pentenyl; in penicillin G, R is benzyl; in penicillin X, R is p-hydroxybenzyl; and in penicillin K, R is N-heptyl. Of these compounds, penicillin X, first isolated by Stodola, Wachtel, and Coghill of the Northern Laboratory, is of unusual interest in that new, highly active penicillins can be produced from it by substitution reactions (Stodola, *et al.*[1]).

A brief summary of the results obtained by British and American chemists was published in *Science* in 1945 by the Committee on Medical Research, O.S.R.D. (Washington) and the Medical Research Council (London); details, however, will not be available until the appearance of the Monograph entitled "The Chemistry of Penicillin," now in preparation under the auspices of the National Academy of Sciences and the Office of Scientific Research and Development, soon to be published by the Princeton University Press. Two short excerpts from this Monograph were published in *Science* in 1947 (**105:** 653–659 and **106:** 503–505).

Penicillinase

Penicillin is rapidly destroyed by enzymes, termed penicillinases, that are elaborated by a number of common Gram-negative and certain Gram-positive species of bacteria. The production, purification, and characterization of penicillinases have been studied by Benedict, *et al.* (1945a), Woodruff and Foster (1945), Perlstein and Liebmann (1945a and 1945b), McQuarrie, *et al.* (1944), and LePage, *et al.* (1946). In the commercial production of penicillin, penicillinase preparations of high purity find an important role in the testing of the drug for sterility. Parallel with investigations on the enzymatic destruction of penicillin, Benedict, *et al.* (1945, 1946b) studied the breakdown of the drug at various temperatures and pH levels.

[1] To be published in the forthcoming Monograph entitled, "The Chemistry of Penicillin."

Penicillin Production by Other Molds

Penicillin, or penicillin-like substances, appear to be produced by all members of the *Penicillium chrysogenum* series (Raper, 1946), and have, in addition, been reported from a number of molds outside this general group. Florey, *et al.* (1944) reported penicillin-like substances from *P. avellaneum* and *P. turbatum*. Working independently, Wickerham confirmed these observations at this Laboratory. Philpot (1943) reported the production of an antibiotic termed "gigantic acid" from *Aspergillus giganteus* Wehmer. Bush and Goth (1943) reported the production of an antibiotic termed "flavicin" from *A. flavus*. McKee and co-workers (1943 and 1944) reported a substance designated "flavicidin" by the same species. Cook and Lacey (1944) reported *A. parasiticus* to produce a substance which they designated "parasiticin." *Aspergillus oryzae* was listed as weakly positive by Waksman and Bugie (1943) and by Foster and Karow (1945). Penicillin-like substances have also been reported from *A. flavipes* by White (1943), Foster and Karow (1945), and Benedict (unpublished notes); from *A. nidulans* by Foster and Karow (1945) and Dulaney (1947a and 1947b); from *A. niger* by Foster and Karow (1945); and from *A. sydowi* by Benedict and by Robbins. Outside of the genera *Penicillium* and *Aspergillus*, Peck and Hewitt (1945) reported the production of a penicillin-like antibiotic by the dermatophyte, *Trichophyton mentagrophytes*. More recently Rode, *et al.* (1947) has shown a similar substance to be produced by the thermophilic fungus *Malbranchea pulchella*.

Production

The commercial production of penicillin was negligible prior to January 1943. In the five month period ending with May 1943, 400 million units were produced, or roughly, enough penicillin to treat 400 hospitalized cases. The meteoric rise in production attained since that date can, we believe, be adequately indicated by listing the monthly production for a given month, *e.g.*, October, over a period of five years:

	Billion units
October 1943	2.8
October 1944	230.0
October 1945	675.0
October 1946	2633.6
October 1947	4745.2
October 1948	8620.5

During the period from June 1943 to October 1947, the price of penicillin dropped from $20.00 per 100,000 units (acknowledged to be less than cost) to about thirty cents (30¢) per 100,000 units. Parallel with the increase in production and the decrease in price, there has been a steady improvement in the quality of the drug manufactured. Penicillin, as marketed in 1943, commonly contained about 100 u/mg. of pure sodium penicillin; today penicillin is generally marketed as a crystalline sodium or calcium

salt of penicillin G and assays in the neighborhood of 1500 u/mg. The value of the penicillin manufactured in the United States in 1947 was estimated at nearly 150 million dollars.

The production of penicillin on a commercial scale has been reported by Challinor and McNaughton (1943), Elder (1944), McKeen (1944), Callaham (1944), and Coghill and Koch (1945). The reader is referred to these papers for information regarding practices and problems of the manufacturing industry.

Uses

Penicillin is the drug of choice in the treatment of many types of bacterial infection. It is not a cure-all, however, and it is of little or no value in the treatment of many serious diseases. Generally speaking, its application can be correlated with the identity and character of the pathogen. It is particularly effective against the pyogenic cocci and the Gram-positive, spore-forming bacilli, including the anaerobic forms belonging to the genus *Clostridium*. Some of its major applications and limitations are presented in the accompanying table.

An enormous literature has developed on the clinical use and application of penicillin since 1941. For information regarding its use in medicine the reader is referred to works by Herrell (1945), Kolmer (1945), Fleming (1946), and to the vast number of papers that have appeared during the past five years in the Journal of the American Medical Association, the Lancet, and other medical journals.

Applications and Limitations of Penicillin[2]

Penicillin is the most effective drug for the treatment of the following conditions:

Staphylococcic infections, including:
- Carbuncles, boils, other abscesses
- Acute and chronic osteomyelitis
- Meningitis, pneumonia and septicemia
- Sinus thrombosis
- Wound or burn infections

Clostridial infections, including:
- Gas gangrene
- Tetanus

Hemolytic streptococcic infections, including:
- Mastoiditis, peritonitis and septicemia
- Pneumonia, empyema and endocarditis
- Childbed fever

Anaerobic streptococcic infections:
- Childbed fever
- Localized infections elsewhere

Pneumococcic infections of the:
- Meninges, pleura, endocardium, and lungs (especially sulfonamide resistant pneumonia)

Gonococcic infections, particularly sulfonamide resistant gonorrhea

All cases of anthrax

Meningococcic infections not responding to sulfonamides

Bacterial endocarditis due to penicillin sensitive organisms

Vincent's infection

Penicillin is effective in the treatment of the following diseases, but its ability to effect complete cures has not been established:
- Syphilis—especially in early stages

[2] Taken largely from a brochure with annotated bibliography, entitled "Penicillin," published in 1945 by Merck and Co., Rahway, N. J.

Diphtheria, especially in horse-serum sensitive patients
Actinomycosis

Penicillin is not effective in the treatment of the following conditions:

All Gram-negative bacillary infections:
Eberthella typhosa (typhoid fever)
Salmonella schotmülleri (paratyphoid A)
Shigella dysenteriae (bacillary dysentery)
Escherichia coli
Haemophilus influenzae
Bacillus proteus
Pseudomonas pyocyaneus
Brucella melitensis (undulant fever)
Pasteurella tularensis (tularemia)
Klebsiella pneumoniae (Friedländer's bacillus)
Tuberculosis
Histoplasmosis
Acute rheumatic fever
Hodgkin's disease
Acute and chronic leukemia
Ulcerative colitis
Coccidioidomycosis
Malaria
Poliomyelitis
Blastomycosis
Moniliasis
Virus infections (with the possible exception of ornithosis and psittacosis)
Cancer

Penicillin is of questionable value in mixed infections in which the predominating organism is Gram-negative, such as:
Ruptured appendix
Liver abscess
Urinary tract infection
Rat-bite fever due to *Streptobacillus moniliformis*

In the field of veterinary medicine, the most successful application of penicillin has been made in the treatment of bovine mastitis in which the causative organisms were *Staphylococcus aureus*, *Streptococcus agalactiae*, *Strep. dysgalactiae*, and *Strep. uberis* (Slanetz and Allen, 1945). Streptococcic infections respond to smaller doses than those in which the invading organism is *Staph. aureus*. The penicillin solution is administered through the teat canal immediately after a milking period, and apparently has no adverse effects on the mammary glands or on the quality of the milk.

Some investigations have indicated the possible usefulness of penicillin for combating certain plant diseases (Brown and Boyle, 1944 and 1945). Such studies, however, have been limited in number and need to be performed on a much more extensive scale before any conclusions can be reached regarding the usefulness of the drug in this field.

The addition of penicillin to milk and other highly perishable food products has been recommended, but its usefulness as a food preservative is questioned by Curran and Evans (1946). Penicillin in low concentrations will inhibit the growth of many bacteria responsible for food spoilage. It is not effective, however, in preventing the growth of other forms often equally responsible. Gram-negative species are usually not affected, and among the Gram-positive forms, which are generally penicillin sensitive, a number of spore-formers, such as *Bacillus cereus*, produce abundant penicillinase which rapidly destroys the drug. While the addition of penicillin may, under certain conditions, extend somewhat the useful life of a product such as milk, the varied microflora normally present precludes its continuing effectiveness.

PART II

THE MANUAL PROPER

Chapter VI

USE OF THE MANUAL

The purpose of this Manual is two-fold. First, it is designed to facilitate the identification of Penicillia as these are isolated from nature, and as they are encountered, or utilized, in the laboratory, in agriculture, or in industry in connection with special problems. Second, it is designed to introduce to the user a summary of whatever information has accumulated regarding the physiology, biochemistry, pathogenicity, or other characteristics of individual species and groups. The latter type of information is given special consideration under paragraphs entitled "Occurrence and Significance" at the close of each series discussion. Often additional references covering the same type of subject matter are included in the Topical Bibliography (Chapter XVI).

In this Manual, recognized species of *Penicillium* are considered in limited groups, or *Series*, which for the most part are believed to represent natural groupings. Series believed to be naturally related are in turn grouped to form larger subdivisions, or *Sections*. The identification of species is important and should be accomplished wherever possible. Fortunately, for many types of work, recognition of the series is sufficient to characterize general cultural and morphological structures, and oftentimes to indicate general physiological behavior as well. For this reason, and because of intergradations between closely related species, the series concept is stressed particularly.

Data for Identification

In a very limited number of cases Penicillia can be correctly assigned to series or even to species by the examination of specimens taken directly from naturally moldy materials. In the vast majority of cases, however, cultivation in the laboratory under standardized conditions is imperative. To identify successfully any *Penicillium*, certain information must be obtained and carefully analyzed. To facilitate the collection of this essential information we have found a standardized data sheet to be most useful. This guarantees that all pertinent information will be included, and also insures that this data will be listed in a uniform and orderly manner. The information collected should present a comprehensive picture of the cultural and microscopic aspects of the strain being studied or identified. The comparison of different species, or the comparison of unidentified strains with recognized species, is thus greatly facilitated.

For convenience, essential data may be indicated vertically upon a

descriptive sheet elaborate enough to include all observations that may prove useful in diagnosis. A sample descriptive sheet is presented below. Dimensions should be given as ranges established by the examination of many units, not as precise measurements of individual cells or structures, or as decimal values obtained by averaging a large number of separate measurements. Colors should be cited as duplicating or approximating specific plaques or tabs in some recognized color manual such as Ridgway's "Color Standards and Nomenclature" (1912), or as a particular range covered by a series of such tabs.

DESCRIPTIVE SHEET

Cultural and Microscopic Characteristics of *Penicillium* ———

Culture No. (or other designation): *Source:*

Substratum: *Date:* *Age:* *Incub. Temp.:*

Colony Characteristics, including:
Rate of growth—whether spreading or restricted:
Character of growth—whether velvety, floccose, funiculose, or fasciculate; zonate or azonate, etc.:
Character of margin:
Amount of sporulation:
Colony color and color changes during growth period:
Transpired drops (exudate)—abundance and color:
Odor—characterization if possible:
Colony reverse—color and color changes:

Conidial Stage:
Penicilli:
Manner in which borne:
Color:
Dimensions: Overall (high dry):
Spore bearing apparatus (oil):

Conidiophore:
Origin and character:
Surface markings, if any:
Length and diameter below penicillus:

Branches:
Usual number and arrangement:
Dimensions:

Metulae:
Usual number and arrangement:
Dimensions:

Sterigmata:
Usual number and arrangement:
Dimensions:

Ascosporic Stage:
Perithecia:
Relative abundance:
Character and color:
Dimensions:
Pattern of perithecial initials if determinable:

Conidia:
Form and markings:
Dimensions, range:
Arrangement of chains:

Sclerotia:
Abundance and manner in which borne:
Character, form, and measurements:

Asci:
Form and dimensions:
Origin, in chains or single:

Ascospores:
Pattern and markings:
Dimensions:

Significance in nature and relation to special substrata if known:

In the preparation of any species diagnosis, or in the identification of any given strain, some of the above information may not prove significant, hence its inclusion in a description may be unnecessary. The information should, however, be routinely obtained, for only in this way can non-essentials be omitted.

With such a descriptive sheet before him, properly completed for a particular strain, the worker should not experience too great difficulty in locating the section of the genus and the general series to which his *Penicillium* belongs. Within the series, correct assignment to the proper species may be reached through the series key and by carefully comparing the data for his strain with that contained in the descriptions of recognized species. Unfortunately, many of the separating characters which have to be used in the genus *Penicillium* are not exact and clean-cut. Furthermore, the genus is characterized by great variability and intergradation between different strains and species. For these reasons, difficulties will be encountered. In the assignment of an unidentified strain to a certain series, and especially to a particular species, it will often become necessary to explore two or three possible assignments before reaching a decision as to which represents the correct one. The placement of some species is unquestionably arbitrary, but in these cases we have attempted, by cross-keying and otherwise, to indicate other possible areas of relationship.

Bases of Classification

An ideal classification of the genus *Penicillium* should, theoretically, be based upon the development of perithecia, since the occurrence and pattern of a perfect stage is generally accepted as the deciding factor in determining true relationships among the fungi. Furthermore, such a stage is, as a rule, sufficiently conspicuous and distinctive to greatly facilitate identification at all levels of classification. There can be little doubt but that if all Penicillia produced an ascosporic stage we would be in position to present a less arbitrary and probably a briefer, taxonomy of this difficult genus. All of the Penicillia, however, do not develop ascospores. In fact, only a relatively small percentage of the known species have a perfect stage. The vast majority of the strains which are significant in agriculture or in in-

dustry, or which show unique biochemical activities, have not been found to produce perithecia or ascospores in spite of diligent search and experimentation. The student or investigator concerned with the distribution and activities of the Penicillia must, therefore, find some basis other than the development of an ascosporic stage for the separation and identification of his species.

An obvious alternate choice is to use the asexual conidium-producing structures, or penicilli. This is precisely the course that has been followed by all investigators since Link established the genus *Penicillium* in 1809. Brefeld (1874), Zukal (1890), Wehmer (1893), Klöcker (1903), Dangeard (1907), Thom and Turesson (1915), Lehman (1920), and others have described ascosporic species and added these to Link's genus without seriously considering the separation of such forms from the vastly greater number of asexual species. The genus *Penicillium* is regarded as properly assigned among the Ascomycetes despite the fact that most species fail to show an ascosporic phase, and despite the additional fact that in the taxonomy of the genus conidial structures are generally regarded as outweighing perithecia in indicating broad relationships.

Systems of classification proposed by earlier investigators have proved inadequate, hence have undergone frequent change or amendment. The system proposed by Thom in 1930 may in time also prove inadequate. However, it has been generally adopted in this country and abroad, and has furnished a working basis for the identifications necessary to intelligent discussion and reporting of species of Penicillia in relation to practical problems and applications. With minor emendations to include additional species described since 1930, and with certain changes dictated by the continued comparative study of species already known, Thom's bases of separation within the genus as proposed in his Monograph (1930) are followed in the present Manual.

The primary basis of separation within the genus Penicillium rests upon the pattern and complexity of the conidial structure, or penicillus. Upon this criterion four (4) major sections are established as follows:

Monoverticillata: Conidial structures typically consist of a single verticil of sterigmata, or conidium-bearing cells, terminating a fruiting branch, or conidiophore (fig. 8). The conidiophores may arise directly from mycelia contained in the substratum, or as lateral branches from aerial hyphae, variously interwoven or less commonly arranged in more or less well-defined ropes. In certain forms the conidiophores are irregularly branched but the individual fruiting structure still retains its basic monoverticillate character. Wehmer, followed by Sopp, Bainier, and others, referred monoverticillate species to the genus *Citromyces*. Thom (1930)

abandoned this practice since no satisfactory line of separation could be found which differentiated between the truly monoverticillate forms and the simpler of the biverticillate types.

Asymmetrica: Conidial structures are characteristically once- or twice-branched below the level of the sterigmata and are typically asymmetrical (fig. 9). The metulae, cellular elements bearing the sterigmata, occur in verticils terminating the main conidiophore only, or the main conidiophore axis and one or more branches arising from it at the next lower node. This section embraces the larger portion of the genus *Penicillium*, hence has to be subdivided into sub-sections upon other characteristics. Intergradation between this section and the Monoverticillata seem to occur through at least two series of species, whereas other species appear to be transitional between this section and the Biverticillata-Symmetrica.

Biverticillata-Symmetrica: Conidial structures typically consist of single terminal verticils of metulae, each bearing crowded verticils of sterigmata that are characteristically lanceolate in pattern with acuminate conidium-bearing tips (fig. 10). The over-all appearance of the typical penicillus gives the impression of a fairly compact and completely symmetrical brush or broom. Fractional penicilli are produced, in certain species, but even here the characteristic pattern of the cellular elements, particularly the sterigmata, is preserved. Species assignable to this section quite commonly produce abundant yellow pigmented hyphae and oftentimes produce a strong pigmentation in the colony reverse and agar which ranges from yellow through deep orange to bright red. Wehmer (1914) proposed the name Verticillatae for this section of the genus; Biourge (1923) designated it as a sub-genus *Biverticillium*; whereas Thom first discussed it as the *Penicillium luteum-purpurogenum* group in 1915 and subsequently (1930) adopted the name used here.

Polyverticillata: Thom (1930) created this section to include certain species described by Bainier (1906 and 1907) which are characterized by penicilli that are usually symmetrical and which are branched at several levels below the sterigmata. Conidiophores are regularly short and heavy, and the cellular elements in the branching system are likewise typically short and comparatively thick (fig. 168). Members of the section are seldom encountered in culture. Type material has not been available for study and the true relationship of these forms is not known. Their assignment here is dictated solely by the development of much branched penicillate conidial structures. Other forms, more or less similarly branched, have apparently been assigned to *Scopulariopsis*.

"Related Genera": Certain forms develop penicillate conidial structures but differ from *Penicillium*, in the generally accepted sense, sufficiently to

be excluded from that genus. Other genera which have been commonly discussed as Penicillia include *Gliocladium* Corda (figs. 169 and 170), *Paecilomyces* Bainier (fig. 171), and *Scopulariopsis* Bainier (fig. 172).

The above separations are admittedly arbitrary, and intergrading forms are found which bridge between the various sections as proposed. Specific examples of transitional forms will be brought out in the discussions that follow.

Even though the most striking and the most stable characteristics available are employed for separation, forms of intermediate or uncertain relationships are regularly encountered and sharp lines often cannot be drawn between the major sections or, for that matter, between sub-sections, series, or even species. Successful taxonomy of the genus, therefore, must depend upon the judgment of the worker as well as adherence to certain rules which are too often rather indefinite when applied.

A second basis of separation hinges upon whether or not perithecia or sclerotia are produced. Perithecia characterize one series in each of the three major sections. Perithecia are basically similar and a degree of close relationship is indicated between the *Penicillium javanicum* series of the Monoverticillata and the *Carpenteles* series of the Asymmetrica. The perithecia developed by *P. luteum* and allied species of the Biverticillata-Symmetrica are, however, quite different from the above and potent arguments have been advanced for taking these forms out of *Penicillium* and assigning them to another genus such as *Gymnoascus*. This view might have merit were it not for the fact that the conidial structures of ascosporic species are often indistinguishable from those of other species in which perithecium formation has not been observed. Furthermore, it is not uncommon for an ascosporic species to lose its capacity to produce perithecia, and thereafter to continue in culture as a conidial strain wholly typical of the Biverticillata-Symmetrica section.

The production of sclerotia approaches that of perithecia in its usefulness as a diagnostic tool. Like perithecia, sclerotia are developed in widely separated areas of the genus *Penicillium*. Unlike the situation in *Aspergillus*, their appearance does not seem to indicate close relationships of the different series where they occur, or to separate the genus into major natural divisions.

A third basis of separation rests in colony characteristics—*i.e.*, primarily in the texture and pattern of the surface, or aerial growth. Sub-sections and series are established upon the following bases: colonies are regarded as velvety if conidial structures arise as a dense stand from a submerged mycelium to produce a velvety effect (fig. 3A); colonies are regarded as lanose if conidial structures arise from a loose or floccose aerial network to produce a cottony, floccose, or lanose effect (fig. 3B); colonies are regarded as funicu-

lose if conidial structures arise largely, or in part, from ropes or bundles of aerial hyphae (fig. 4A); colonies are regarded as fasciculate if conidiophores are aggregated into bundles, fascicles, or coremia to produce a tufted, fasciculate, or coremiform appearance (fig. 4B).

In the Asymmetrica these growth types are especially pronounced and major sub-sections are centered around them. In the Monoverticillata and in the Biverticillata-Symmetrica they are used as a basis for the separation of series. The above characteristics are of great usefulness in the arbitrary system of classification which is of necessity employed in the genus *Penicillium*. They are not, however, fixed either in character or continuity. For example, strains of some species which are characteristically velvety when freshly isolated, may, through progressive variation in laboratory culture, develop into forms that are essentially floccose or funiculose. On the other hand, strains which are at first strongly fasciculate may lose their capacity to produce conidiophores in bundles or fascicles and hence assume a velvety appearance. Other shifts in colony character may likewise occur. In the presence of such changes in pattern of growth the use of colony texture must be tempered by the best judgment of the worker and correct assignment of the strain or species must depend upon a careful analysis of the total cultural and morphological characteristics of the particular organism.

Additional bases of separation are useful within the different sub-sections and series. These may hinge upon the pigmentation of conidial areas and colony reverse; upon the rate of growth on common laboratory media; or upon the pattern assumed by mature conidial chains, i.e., whether they remain adherent into columns, become widely divergent, or irregularly tangled. Again separation may depend upon the detailed structure of the penicillus, the pattern or character of the sterigmata, the form and markings of the conidiophores, or the shape and dimensions of the conidia.

Series

Individual strains, or aggregates of strains, in *Penicillium* are not generally set apart from all other strains sharply enough to guarantee either absolute individuality or complete duplication of forms already encountered. Usually, however, they seem to fall into some general series pattern. When more and more strains are examined, this series pattern tends to become more real, whereas the individuality of specific strains becomes less apparent. Thus, if only a few strains in a limited group, or series, are examined it is often easily possible to recognize several species; if, however, large numbers of strains are isolated and carefully compared, the definiteness of established species boundaries gradually recedes. Finally, it may prove difficult to establish any clear lines of separation, and species, if

established, have to be centered around certain specified strains which are noteworthy either for some historical reason, or are selected as representative of large but generally rather variable groups of strains.

Throughout this study, the existence of limited groups, or series, of Penicillia with broad cultural and morphological characteristics in common has become increasingly clear. As a rule the members of such series likewise show the same general physiological and biochemical characteristics.

Species

What constitutes a species of *Penicillium*? No answer will satisfy all requirements. From the standpoint of the mycologist working in a culture laboratory, however, two or more organisms may be regarded as belonging to the same species if they have the same morphology, including both cultural and microscopic characteristics, and if they agree in such routine reactions as are determinable without the introduction of elaborate quantitative analytical methods.

The extent of variation, to be tolerated, should be based upon repeated parallel cultivation and observation of such organisms upon selected culture media and at different temperatures, to determine the effect of nutritional and environmental factors. All observable information is theoretically valuable, but the physical limitations of the culture room, and the time and energy of the investigator, dictates that comparative cultivation and observation should be generally limited to two or three carefully selected culture media. To undertake to define all possible responses, strain by strain, can easily become an endless operation resulting in the accumulation of vast amounts of data often possessing little real significance.

Cultural appearance and morphology must be expected to vary within a certain range, governed by the limits established for the species, and these limits should represent the product of observation, experience, and good judgment.

Unusual or bizarre structures which are occasionally encountered should not be over-emphasized. The response of a particular organism to a particular environment must not be over-looked, but the unusual must be scrutinized and shown to represent a consistent response to conditions before it warrants inclusion in either description or illustrations. In any elaborate study of a particular species, the range of variation in structure is important. Of greatest importance, however, is the type of organization usually found in the penicillus, and the type of colony development and color production usually encountered in the growing culture.

Too great emphasis must not be placed upon exact measurements or numbers. Ranges of measurements, if carefully arrived at, are far more significant than specific figures. It would be most convenient if branches,

metulae, and sterigmata occurred in three's, four's, or other fixed numbers, but no species of *Penicillium* is so precise in its pattern of development. Specification of the usual number of elements in a verticil is very valuable, but this number should not be drawn in too specific terms if it is to be representative of a normal preparation rather than of a few selected fruiting structures.

Too great emphasis should not be placed upon limited changes in color, amount of sporulation, or other features which may in part reflect changes that are taking place in the culture substratum. Since the mold is usually growing upon a mixture of several fermentable or decomposable materials, the nature of the nutrient substratum may be expected to change from day to day. For example, in the growth of *Penicillia* changes in pH are common and may markedly affect cultural characteristics such as amount of sporulation, intensity of pigmentation, etc.

Too great expectations should not be placed in the continued stability of individual strains in culture, or upon too exact duplication of new isolates assigned to the same species. The existence of great series of related strains, typified by such species as *Penicillium expansum*, *P. chrysogenum*, *P. roqueforti*, *P. terrestre*, and others is evidence that mutability is the rule, rather than the exception, throughout the genus. Strains and species differ. Thom's type of *P. camemberti* (now maintained as NRRL 877, and illustrated in fig. 110C and D) today presents a cultural picture indistinguishable from that developed when it was first isolated in 1904; his type of *P. oxalicum* (now NRRL 787 and illustrated in fig. 100E) isolated at about the same time, lost the most striking characters emphasized in the description within the first dozen transfers. It is today hardly recognizable in culture as the same species, although the pattern and measurements of its conidial structures confirm its identity (see p. 381).

Biochemical reactions, or the elaboration of specific products, often furnish valuable clues to relationships. However, extensive use of such characters would necessitate a quantitative and qualitative study of the biochemical activities of each strain, hence add immeasurably to the task of identification. Furthermore, the capacity of a given strain to produce a specific reaction, or product, often diminishes and may even disappear unless the greatest care is exercised in culture maintenance. It is characteristic of almost all members of the *Penicillium chrysogenum* series to form penicillin, but the amount produced varies from very substantial to practically zero. At the same time, penicillin formation has been demonstrated for *P. avellaneum* (in the Biverticillata-Symmetrica) and *P. turbatum* (in the Monoverticillata). The usefulness of biochemical identity as a decisive criterion in the taxonomy of molds is open to serious question.

With few exceptions the descriptions of species as presented in this Man-

ual are based upon our own observations of living cultures grown under fairly standardized conditions. Commonly the descriptions are supplemented by pertinent observations made by the species' author, or other investigators, who may have worked with the species or strains in question. If a latin description was given in the original work, this naturally forms the central core upon which recognition is based, or around which it is attempted. Vernacular notes and carefully executed figures often provide additional valuable clues to identity. It is believed that the user of this book will benefit by the presentation of fairly uniform descriptions resulting from broad comparative studies and the presentation of original data in fairly standardized form, rather than by any scheme wherein a maximum amount of the original description might be preserved. In every case we have endeavored to cite the place of species publication in order that the user of the Manual may consult the original paper if needed.

The standardized species description should specify the substratum and temperature used; the texture and appearance of the colony, together with marginal features, zonation if present, etc.; color, including color changes in conidial areas, the colony reverse, and the substratum; the presence or absence of odor and transpired drops, and their characterization if possible; the character of the conidiophore, including its origin, measurement, and wall markings if any; the penicillus, with its branching system, including metulae, and sterigmata; conidia and conidial chains; perithecia or sclerotia, if present, with whatever distinguishing features they may exhibit; and finally, any conspicuous feature of metabolism that is known.

Over a period of many years, we have used Czapek's solution agar (see p. 64) more than any other for the general study of species of *Penicillium*. It is readily prepared; it should not differ materially in different laboratories; its reaction is almost neutral; it is colorless, hence reveals color changes due to the mold growth; and most species of *Penicillium* grow moderately well upon it. It is not suitable for the cultivation of perithecial forms, and occasional species and strains which suffer from some nutritional deficiency make at best a very sparse and atypical development upon it. In the current study we have routinely cultivated strains in parallel upon Czapek's agar, Czapek's agar containing one per cent corn steep liquor (termed steep agar), and malt extract agar. The latter medium is especially favorable for ascosporic strains. The addition of the steep liquor to Czapek's agar supplies vitamins, essential amino acids, etc. that are necessary for the growth of some forms.

Varieties

The taxonomic term *variety*, is little used in this Manual. Whenever it occurs, it is intended to distinguish some particular strain, or group of

strains, which differ from a well-recognized species in some marked characteristic. For example, the usage *Penicillium cyclopium* var. *echinulatum* is introduced to include a limited number of cultures showing all of the essential characteristics of *P. cyclopium* except that they produce unusually roughened conidiophores and globose rough conidia. The term variety is only useful for recognizing a clearly defined variation in color, colony habit, or structure within an otherwise homogenous species.

Mutants

The term *mutant*, is nowhere used in this Manual to designate a taxonomic entity. It is, however, commonly employed as a designation for strains of known origin which develop inherited characters differing sharply from those of the parent strain and species. If the source of a mutant, or mutation, were unknown, the taxonomist would probably recognize it as a species or variety, depending upon the character and importance of the change encountered. For this reason, studies in experimental evolution may soon necessitate some form of taxonomic recognition of artificially induced mutants.

Strains

The term *strain* is commonly used in this text, and refers to a particular isolate selected and maintained under a name, number, or laboratory symbol which insures identity. Such an organism may be wholly typical of some particular species, or it may represent a variant distinguished by unique cultural or microscopic characteristics. It may be obtained by direct isolation from some natural source, or it may originate as a sub-culture from an organism significant in some current investigation. In any case it represents as nearly as possible a continuation in culture of some selected cultural entity. Complete identity of many strains may be encountered when these arise from individual conidia of some heavily sporing and seemingly stable parent. Minor or conspicuous differences may be expected among strains representing isolates from widely separated or markedly different sources. Differences may likewise be expected among strains derived from parent cultures which show moderate to marked instability in laboratory culture.

An individual strain may be either worthless or very valuable. If a strain is important because of its biochemical potentialities, or because of research that may have been based upon it, that strain should be maintained with punctilious care. It should be maintained as free from variation or loss of vitality as possible since valuable stocks can seldom be reisolated or reidentified with certainty from new materials. Other suitable strains may be found or developed, but this usually requires much time

and effort. Even then, exact duplication of morphology or biochemical activity is usually not achieved.

New Species

Individual strains, or groups of strains, are occasionally encountered which differ from all recognized forms sufficiently to warrant the description of new species. Usually such forms can be diagnosed as belonging to one or another of the general series which constitute the genus. Careful consideration and detailed comparison of related species in culture, together with extensive review of the published literature, must precede any thought of species description. The worker should realize that *many* species of *Penicillium* have already been described by *many* mycologists in *many* different laboratories working over a period of *many* years. Of course this does not mean that new material warranting description will not be encountered, particularly when special types of natural substrata are intensively examined, or when out-of-the-ordinary techniques of isolation are employed. It does mean, however, that one should have a full appreciation of earlier taxonomic studies in the genus, and that one should exercise the greatest possible care to avoid replication of such studies.

Recognized Species

Of more than seven hundred species of *Penicillium* that have been described, a total of 137 are recognized in this Manual. The authors realize that mistakes have undoubtedly been made. In some cases valid species may have been reduced to synonymy through our lack of understanding of the true characteristics of the species as originally described. In other cases we may have selected for continued recognition species which were originally too vague and indefinite to warrant species status. Throughout the study we were motivated by the firm conviction that much duplication in description had undoubtedly taken place in different laboratories where comparable source materials were not studied. Furthermore, we were convinced that no mycologist could hope to distinguish between all of the forms that have been described. In large measure, the development of a satisfactory and useful taxonomy of the genus *Penicillium* seemed to hinge upon two premises: First, that the number of species of *Penicillium* was too large and must be reduced; and second, that the species selected for continued recognition should be presented in as tangible, specific, and reproducible terms as possible.

Throughout our study we have endeavored to recognize those species which, by priority or common usage, have come to be most generally accepted. Furthermore, we have endeavored to center the description and discussion of recognized species around the type strains of such species un-

less these clearly failed to represent the original concept, in which case some more recent isolate, or isolates, regarded as truly representative was selected for this purpose. We have had available for this study a wealth of living material (see pp. 87–88), including the types of many, if not an actual majority, of the species considered. Type material has often been available for both the species recognized and others reduced to synonymy. It has perhaps been the detailed observation of such types as often as the analysis of published descriptions which has governed our decisions regarding species recognition on the one hand and synonymy on the other.

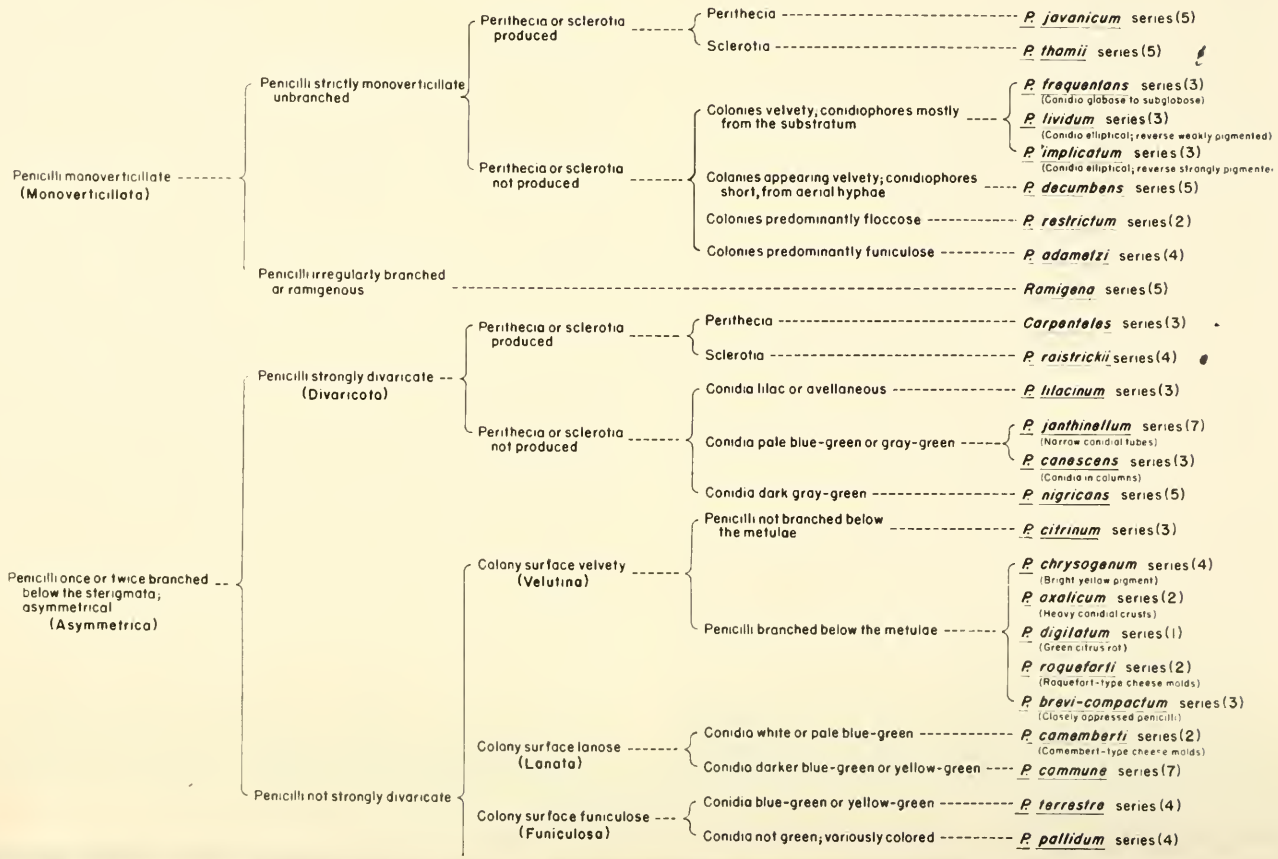
Species that are not recognized as valid have been handled in one of two ways. If the species is represented in culture collections by named specimens, or if it has been reported in the literature fairly commonly, it is discussed in a short paragraph following the species with which it is regarded as probably synonymous. Specific reasons for our course of action are usually cited. If the species was not originally described in tangible terms, and if it has not been generally accepted or reported in the subsequent literature, it is listed only in the Species Index at the end of the Manual (Chapter XVIII). Our opinion, if any, as to the probable relationship or synonymy of the species is given there.

Keys

The number of recognizable species of *Penicillium* is too large for all of them to be conveniently included in a single key. Furthermore, in tracing the identity of any given strain or culture we believe that it is neither necessary nor desirable to handle large portions of a key which are irrelevant to the task in hand. For this reason, we shall introduce here only general keys to the major subdivisions of the genus and to the series which comprise them. Once the suspected series relationship of the unidentified culture is decided upon, the user can quickly determine the probable correctness of such placement by examining (1) the list of "outstanding characters" and (2) the series key, both of which appear at the beginning of each series discussion.

The first key is presented in diagrammatic form (fig. 33) and is designed to enable the worker to quickly determine the probable broad relationships of his *Penicillium*. Space limitations prevent us from including in such a key much information of real diagnostic value, hence it will oftentimes prove inadequate and indecisive. Under these conditions the user should immediately go to the written "General Key to Series" which follows, and if necessary to the more detailed keys which introduce the various sections and sub-sections. Despite its recognized shortcomings, the diagrammatic key is presented in the belief that it will generally facilitate identifications.

The second key, or the "General Key to Series," is presented in conven-


Penicilli monoverticillate (Monoverticillata)
Penicilli strictly monoverticillate unbranched
Perithecia or sclerotia produced
Perithecia
P. javanicum series (5)
Sclerotia
P. thomii series (5)
Perithecia or sclerotia not produced
Colonies velvety, conidiophores mostly from the substratum
P. frequentans series (3)
(Conidia globose to subglobose)
P. lividum series (3)
(Conidia elliptical; reverse weakly pigmented)
P. implicatum series (3)
(Conidia elliptical; reverse strongly pigmented)
Colonies appearing velvety; conidiophores short, from aerial hyphae
P. decumbens series (5)
Colonies predominantly floccose
P. restrictum series (2)
Colonies predominantly funiculose
P. adametzi series (4)
Penicilli irregularly branched or ramigenous
Ramigena series (5)
Penicilli once or twice branched below the sterigmata; asymmetrical (Asymmetrica)
Penicilli strongly divaricate (Divaricata)
Perithecia or sclerotia produced
Perithecia
Carpenteles series (3)
Sclerotia
P. raistrickii series (4)
Perithecia or sclerotia not produced
Conidia lilac or avellaneous
P. lilacinum series (3)
Conidia pale blue-green or gray-green
P. janthinellum series (7)
(Narrow conidial tubes)
P. canescens series (3)
(Conidia in columns)
Conidia dark gray-green
P. nigricans series (5)
Penicilli not strongly divaricate
Colony surface velvety (Velutina)
Penicilli not branched below the metulae
P. citrinum series (3)
Penicilli branched below the metulae
P. chrysogenum series (4)
(Bright yellow pigment)
P. oxalicum series (2)
(Heavy conidial crusts)
P. digitatum series (1)
(Green citrus rot)
P. roqueforti series (2)
(Roquefort-type cheese molds)
P. brevi-compactum series (3)
(Closely appressed penicilli)
Colony surface lanose (Lanata)
Conidia white or pale blue-green
P. camemberti series (2)
(Camembert-type cheese molds)
Conidia darker blue-green or yellow-green
P. commune series (7)
Colony surface funiculose (Funiculosa)
Conidia blue-green or yellow-green
P. terrestre series (4)
Conidia not green; variously colored
P. pallidum series (4)

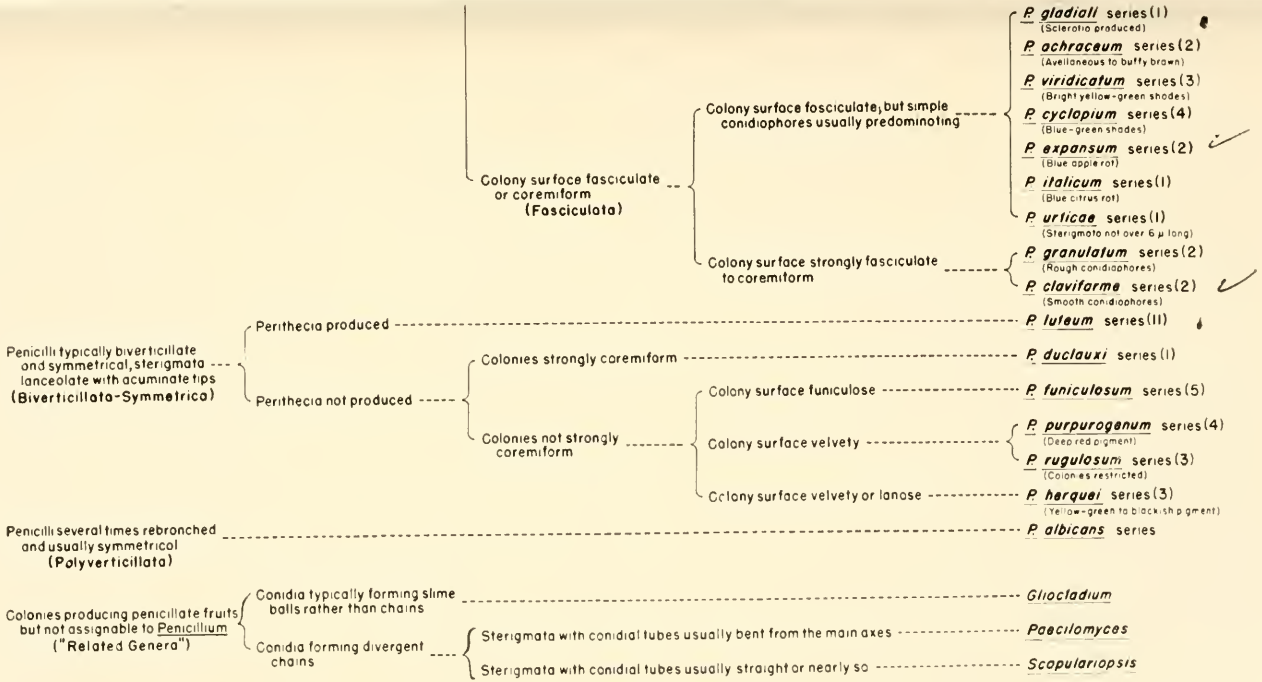


FIG. 33. Diagrammatic key to major subdivisions and series within the genus *Penicillium*. Numerals following series names indicate the number of species included in each series.

tional manner, is more detailed, and should enable the worker to determine the probable series relationships of the form under observation, or at least to narrow the possibilities down to two or three such series. Further steps toward identification are made by means of the keys to individual series, or to sections and sub-sections when questions arise regarding the correctness of presumptive series assignment.

Page

General Key to Series

I. Penicilli consisting of single clusters, or verticils of sterigmata at the tips of fertile hyphae, or conidiophores; conidiophores usually unbranched, in some forms irregularly branched but with each branch terminating in a distinct and separate monoverticillate penicillus
MONOVERTICILLATA Section 126

A. Colonies producing either perithecia or sclerotia.

1. Colonies producing fertile perithecia which are commonly sclerotioid and often ripen late..... *P. javanicum* series 132

2. Colonies producing sclerotia, often suggestive of young perithecia but never developing an ascogenous stage..... *P. thomii* series 154

B. Colonies producing neither perithecia nor sclerotia.

1. Conidiophores generally unbranched and bearing single, strictly monoverticillate penicilli.

a. Colonies velvety or nearly so; conidiophores arising mostly from the substratum.

1′. Colonies generally spreading broadly.

aa. Conidia globose or subglobose..... *P. frequentans* series 170

bb. Conidia elliptical..... *P. lividum* series 189

2′. Colonies growing rather restrictedly, especially on Czapek's solution agar..... *P. implicatum* series 196

b. Colonies appearing velvety or lightly floccose, but with conidiophores borne as short branches from interwoven aerial hyphae
P. decumbens series 205

c. Colonies floccose or floccose-funiculose with conidiophores arising primarily from aerial hyphae.

1′. Colonies predominantly floccose with funiculose habit lacking or limited..... *P. restrictum* series 222

2′. Colonies with funiculose habit predominant or well-developed
P. adametzi series 227

2. Conidiophores mostly irregularly branched but with each branch bearing a terminal, well-marked monoverticillate penicillus
The Ramigena series 239

II. Penicilli characteristically once- or twice-branched below the level of the sterigmata; typically asymmetrical, irregular, or one-sided; sterigmata not lanceolate..... ASYMMETRICA Section 254

A. Penicilli characteristically strongly divaricate, with individual elements strongly divergent, often appearing monoverticillate but so arranged as to produce the appearance of a single branched penicillus
Divaricata Sub-section 255

1. Colonies producing perithecia, sclerotia, or masses of thick-walled cells.

a. Colonies producing true perithecia, parenchymatous or sclerotioid throughout; ripening from the center outward and often late..... *Carpenteles* series 260

b. Colonies producing sclerotia or masses of thick-walled cells; never developing asci or ascospores..... *P. raistrickii* series 273

2. Colonies not producing perithecia, sclerotia, or masses of thick-walled cells.

a. Conidial areas not showing green, gray-green, or blue-green shades—lilac, vinaceous or avellaneous shades usually produced *P. lilacinum* series 284

b. Conidial areas showing green, gray, gray-green, or blue-green shades.

1′. Conidial areas in pale blue-green or gray-green shades; colony reverse often brightly colored.

aa. Conidial chains strongly divergent; sterigmata abruptly tapered to narrow conidium bearing tubes *P. janthinellum* series 294

bb. Conidial chains tending to form columns, at least when young; sterigmata not abruptly tapered *P. canescens* series 315

2′. Conidial areas in dull gray to olive-gray shades; colony reverse usually in dull yellow to orange-brown shades *P. nigricans* series 323

B. Penicilli seldom strongly divaricate, usually compact, with branches and metulae tending to be parallel rather than divergent.

1. Colonies typically velvety, with conidiophores arising characteristically from the substratum in a dense even stand Velutina Sub-section 336

a. Penicilli seldom branched below the level of the metulae; sterigmata not lanceolate or acuminate..... *P. citrinum* series 338

b. Penicilli commonly branched below the level of the metulae.

1′. Penicilli commonly long, with elements often loosely arranged.

aa. Conidiophores smooth-walled; colony margin not arachnoid.

1″. Colonies typically producing abundant yellow pigmentation in exudate and reverse *P. chrysogenum* series 355

2″. Colonies not producing yellow pigment in exudate and reverse.

aaa. Soil forms..... *P. oxalicum* series 376

bbb. Green citrus rot..... *P. digitatum* series 385

bb. Conidiophores rough-walled; colony margin arachnoid *P. roqueforti* series 392

2′. Penicilli comparatively short, compact, with all elements compressed..... *P. brevi-compactum* series 404

2. Colonies typically lanose or floccose, with conidiophores commonly long, usually arising as branches from aerial hyphae or from the substratum in marginal areas in older colonies... Lanata Sub-section 419

a. Colonies predominantly white and remaining so, or becoming light gray-green with the development of ripe conidia *P. camemberti* series 421

b. Colonies quickly developing some shade of green in conidial areas
P. commune series 429

3. Colonies with surface typically ropy or funiculose from aggregation of aerial hyphae; conidial structures arising primarily from aerial hyphae or ropes of hyphae.....Funiculosa Sub-section 445

a. Conidial areas in yellow-green, blue-green, or gray-green shades; penicilli large as in the Lanata and Fasciculata; conidia subglobose to elliptical.....*P. terrestre* series 446

b. Conidial areas variously colored but never in green shades; penicilli often comparatively narrow; conidia strongly elliptical to cylindrical.....*P. pallidum* series 458

4. Colonies with surface growth appearing mealy, tufted, fasciculate, or coremiform due to aggregation of conidiophores into upright fascicles or bundles.....Fasciculata Sub-section 467

a. Sclerotia characteristically produced.....*P. gladioli* series 471

b. Sclerotia not produced.

1′. Colonies with simple conidiophores and fascicles intermixed, but with simple conidiophores usually predominating.

aa. Conidial areas not developing true green colors in areas of ripe conidia.....*P. ochraceum* series 475

bb. Conidial areas typically in bright yellow-green shades, conidiophores rough.....*P. viridicatum* series 481

cc. Conidial areas typically in blue-green shades with the blue element predominant or at least clearly evident; conidiophores rough or smooth.....*P. cyclopium* series 490

dd. Conidial areas typically in yellow-green or glaucous shades; conidiophores rough or smooth.....*P. expansum* series 508

ee. Conidial areas typically in pale to dull gray-green shades; conidiophores smooth-walled.

1″. Sterigmata usually 8μ or more in length
P. italicum series 523

2″. Sterigmata 6μ or less in length.....*P. urticae* series 531

2′. Colonies with most conidiophores aggregated into fascicles or definite coremia.

aa. Coremia predominating but interspersed with abundant simple conidiophores.....*P. granulatum* series 539

bb. Coremia very prominent, with simple conidiophores lacking or very few in number.....*P. claviforme* series 548

III. Penicilli characteristically biverticillate and symmetrical, but sometimes fractional in some species and strains; sterigmata typically lanceolate, with apices long-tapered, acuminate
Biverticillata-Symmetrica Section 557

A. Colonies producing perithecia or sclerotia.

1. Colonies producing soft perithecia upon most substrata, usually bright yellow in color.....*P. luteum* series 564

2. Colonies producing sclerotia or masses of thick-walled cells, commonly embedded in the substratum
P. novae-zeelandiae (and scattered strains in other conidial series) 665

B. Colonies not producing perithecia or sclerotia.

1. Colonies regularly developing abundant, erect coremia
P. duclauxi series 609

2. Colonies with surface appearing funiculose, floccose-funiculose, or occasionally somewhat tufted.....*P. funiculosum* series 614
3. Colonies with ropiness absent or reduced and with surface typically velvety.
   a. Colonies usually developing an intense red or purple-red pigmentation in mycelium and reverse, with most strains growing fairly rapidly.....*P. purpurogenum* series 631
   b. Colonies never developing an intense red pigmentation, growing very restrictedly upon Czapek and steep agars
   P. rugulosum series 646
4. Colonies comparatively deep, often appearing lanose; with vegetative mycelium typically in yellow-green shades and with reverse often similarly colored.....*P. herquei* series 658

IV. Penicilli large, usually symmetrical, typically branched at three or more levels below the sterigmata.....Polyverticillata Section 668

V. Forms producing conidial structures often more or less penicillate but excluded from the genus *Penicillium*.
   A. Colonies variously colored, in cream to rose or in various green shades; conidial structures usually penicillate but with conidia typically collecting into slime balls rather than remaining adherent in chains; ascosporic stage unknown.....*Glioeladium* Corda 674
   B. Colonies never green; conidial structures often penicillate, but with unusually long sterigmata showing tips characteristically bent away from the main cell axes; ascosporic stage (Genus: *Byssochlamys*) consists of naked asci borne upon fertile hyphae not collected into a perithecium.....*Paecilomyces* Bainier 688
   C. Colonies never showing true greens, ranging from white to tan or rust, through brown to smoke or fuscous shades; conidial structures often more or less penicillate; conidia truncate at base, characteristically showing a basal ring surrounding a germinal pore; ascosporic stage (Genus: *Microascus*) shows dark-walled, ostiolate perithecia
   Scopulariopsis Bainier 694

Chapter VII

MONOVERTICILLATA

The Monoverticillata constitutes an aggregate of series and species bound together by the arbitrary fact that the penicillus consists of a single cluster, or verticil, of sterigmata at the tip of a fertile hypha, or conidiophore. This fertile hypha is usually unbranched, but in those sections in which branching occurs the individuality of the terminal verticil of sterigmata, each producing a chain of conidia, is maintained. Naturally this division of the genus includes the larger part of the species included by Biourge in his subgenus *Monoverticillium*, by Dierckx in *Aspergilloides*, and by Wehmer, Bainier and Sartory, and others in *Citromyces*.

Very few species are absolutely monoverticillate—that is, produce conidiophores entirely without branching below the terminal cell which bears the verticil of sterigmata. In the majority of species, however, only an occasional conidiophore shows a branch bearing a similar penicillus. In a single series, designated the Ramigena, the fertile hypha or conidiophore is nearly always branched at various septa, with the branches varying in length and usually diverging and not assuming the over-all appearance of a characteristic brush or broom. The identity of each branch as a strictly monoverticillate penicillus is usually evident.

In the *Penicillium javanicum* series the species are ascosporic, with perithecia typically developing first as parenchymatous to sclerotioid bodies and subsequently ripening from the center outward. The *P. thomii* series is characterized by the production of true sclerotia which, in appearance and texture, may simulate the perithecia just noted, but which never develop an ascosporic phase.

The name *Citromyces* proposed by Wehmer (1893) was based upon two particular citric acid producing cultures, before he knew the wide range of species which would be included within the morphological limits proposed for his genus. Wehmer's description assumed that the conidiophore was always unbranched, hence produced a single apical verticil of sterigmata. On this basis the line between *Citromyces* and *Penicillium* was sharp.

Sopp (1912) and Bainier and Sartory (1912 and 1913) used the name *Citromyces*. Dierckx created his subgenus *Aspergilloides* for the whole group of monoverticillate forms. Biourge used the name *Aspergilloides* in his discussion on page 31 (Monograph, 1923) and proposed the subgenus *Monoverticillium*. He made the characterization broad enough to include all species in which the individuality of the ultimate verticil of sterigmata was maintained, even though its stalk had become a part of a fairly definite

branching system. Westling and Thom merely dropped the name *Citromyces* and called all of them species of *Penicillium*.

Although the marks of division may be more or less unsatisfactory at times, the individuality of each verticil of sterigmata with their conidial chains is a character usually readily recognized when a growing culture in a petri dish is viewed with low magnifications of the compound microscope. For the purposes of our discussion, separation between the monoverticillate group and the remainder of the Penicillia is based upon examination of the terminal verticil of the main conidiophore. If there are no branches at the apex of the main axis, or if each branch maintains fairly definite individuality, *i.e.*, produces a separate penicillus, the species is assigned to the Monoverticillata.

However, no sharp line of separation can be drawn between the Monoverticillata and either the Velutina or the Divaricata sub-sections of the Asymmetrica. Complete bridging is effected between the Monoverticillata and the Velutina through the Ramigena series and *Penicillium corylophilum* in the *P. citrinum* series. A similar transition from the Monoverticillata to the Divaricata occurs through *P. jenseni* Zaleski. Additional evidence of close relationship between the Monoverticillata and the Divaricata rests in the similarity of perithecia and sclerotia in the two sections. A rigid separation into monoverticillate and biverticillate forms is thus unattainable in fact, and one is led to recognize that the different sections of the genus *Penicillium* are intimately related and represent merely different facets of a large and variable group of molds.

Key to the Monoverticillata

I. Colonies producing perithecia or sclerotia.
  A. Colonies producing fertile perithecia, but perithecia often ripening late.
    1. Perithecia firm or sclerotioid at first, ripening from the center outward.
      a. Penicilli monoverticillate or fragmentary . . . . *P. javanicum* series 132
        1′. Colonies producing abundant red to reddish brown pigment upon most substrata.
          aa. Ascospores lenticular, about 2.5 to 3.0μ in long axis, with equatorial ridges generally lacking and furrow often evident only as a line, with walls finely roughened *P. javanicum* van Beyma 135
          bb. Ascospores lenticular, about 2.0μ in long axis, with prominent equatorial ridges and furrow, with walls roughened *P. parvum* Raper and Fennell 138
        2′. Colonies not producing abundant reddish or reddish brown pigment upon most substrata.
          aa. Ascospores lenticular, about 3.0 to 3.5μ in long axis, with furrow evident but not pronounced, with walls finely echinulate; penicilli typically monoverticillate *P. brefeldianum* Dodge 141

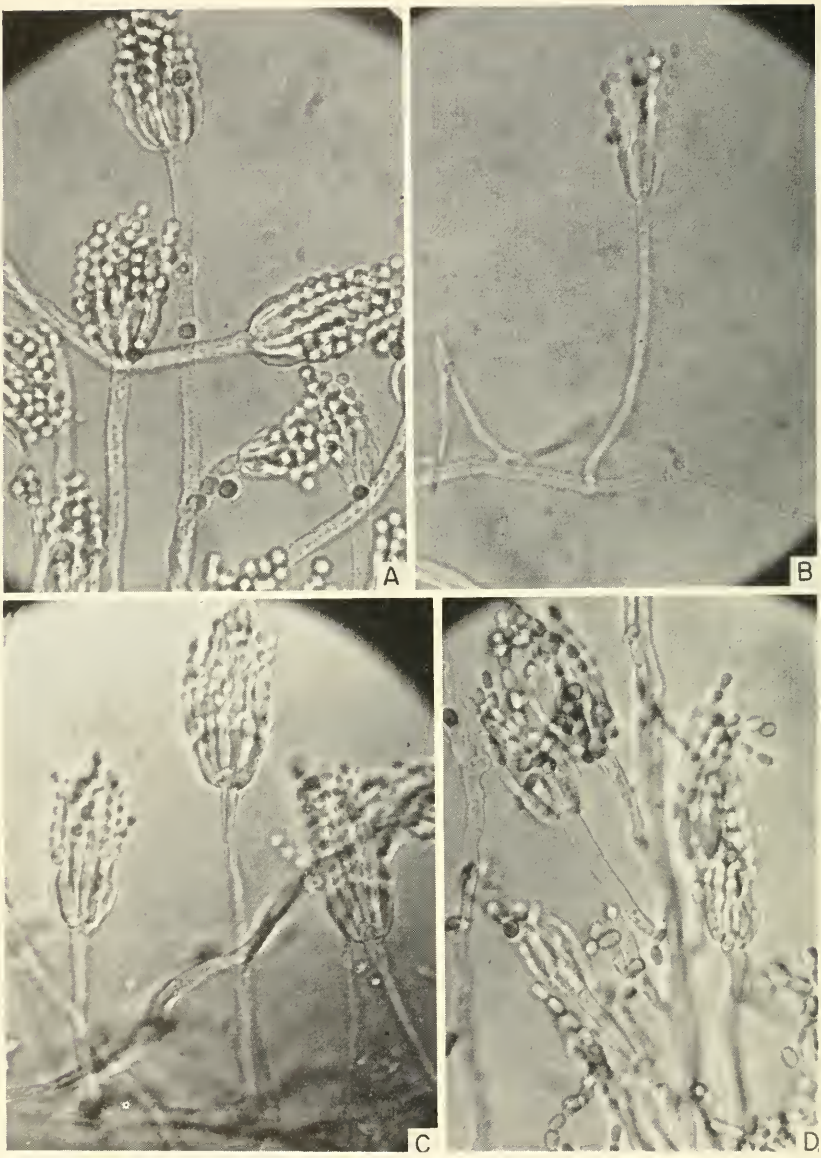


FIG. 34. Types of penicilli in the Monoverticillata. *A*, Penicilli borne singly upon conidiophores arising mostly from the substratum, *Penicillium frequentans* Westling, NRRL 1915. *B*, Delicate penicillus of *P. javanicum* v. Beyma, NRRL 707. *C*, Penicilli borne on short branches (conidiophores) from interlacing aerial hyphae, *P. chermesinum* Biourge, NRRL 2048. *D*, Penicilli borne upon short branches arising irregularly from an ascending fertile hypha, *P. capsulatum* Raper and Fennell, NRRL 2056. *B* on hay agar, *A*, *C*, and *D* on malt; all × 900.

bb. Ascospores lenticular, about 3.5 to 4.0μ in long axis with walls strongly echinulate and furrow generally pronounced; penicilli reduced or fragmentary
P. chrlichii Klebahn 146

cc. Ascospores lenticular, about 4.0μ in diameter, not furrowed or showing only an equatorial line, with walls smooth; penicilli very reduced, often appearing as single sterigmata ..... *P. levitum* Raper and Fennell 148

b. Penicilli typically biverticillate but with monoverticillate structures produced, and with perithecia at first sclerotioid and ripening late ..... Carpenteles series 260
(in the Divaricata, pp. 260–273)

2. Perithecia soft, loose-textured, without a definite or firm outer wall; penicilli commonly fragmentary, often appearing monoverticillate.

a. Ascospores large, 7.0 to 8.5μ in long axis, broadly elliptical, with 5 to 8 prominent longitudinal flanges or ridges showing in side view, without definite equatorial furrow
P. striatum Raper and Fennell
(in *P. luteum* series)

b. Ascospores small, 2.8 to 3.2μ in long axis, with a single equatorial ridge or two ridges closely appressed ..... *P. stipitatum* Thom
(in *P. luteum* series)

B. Colonies producing sclerotia, often suggestive of young perithecia but never developing an ascogenous stage.

1. Penicilli strictly monoverticillate.

a. Sclerotia produced upon all substrata, hard, brittle, crushing with difficulty, composed of thick-walled sclerenchyma-like cells
P. thomii series 154

1′. Sclerotia borne in clusters of varying size, surrounded by conspicuous envelopes of bright orange-red mycelium, characterizing the colony on some substrata
P. sclerotiorum van Beyma 160

2′. Sclerotia in pink shades, not in clusters and not embedded in masses of orange-red hyphae ..... *P. thomii* Maire 156

3′. Sclerotia in orange-brown shades, not in clusters, often surrounded by a loose network of yellow to orange or light brown mycelium ..... *P. lapidosum* Raper and Fennell 163

b. Sclerotia produced upon some substrata, not on others including Czapek, comparatively soft, composed of pseudo-parenchymatous cells with walls thickened ..... *P. turbatum* sub-series 166

1′. Colonies on Czapek agar not developing dull, dark purple colors in reverse, somewhat restricted ..... *P. turbatum* Westling 166

2′. Colonies on Czapek agar developing dull, dark purple colors in reverse, very restricted ..... *P. pusillum* Smith 167

2. Penicilli typically biverticillate-asymmetric ..... *P. raistrickii* series
(in the Divaricata, pp. 273–283)

II. Colonies not producing perithecia or sclerotia.

A. Conidiophores generally unbranched and bearing single, strictly monoverticillate penicilli.

1. Colonies velvety or nearly so, with conidiophores arising mostly from the substratum.

a. Colonies generally spreading broadly on most media.
1′. Conidia globose to subglobose.....*P. frequentans* series 170
aa. Colonies with conidial areas strictly velvety and with reverse usually in orange-brown to reddish purple shades.
1″. Conidia mostly 2.5 to 3.5μ, with walls thin, smooth, or finely roughened.....*P. frequentans* Westling 172
2″. Conidia mostly 4.0 to 5.0μ, with walls heavy, dark green, and coarsely roughened
P. purpurrescens (Sopp) n. comb. 177
bb. Colonies with conidial areas strictly velvety and with reverse usually in bright orange-red to red shades
P. multicolor G.-M. and P.
(see *P. implicatum* series, p. 196)
cc. Colonies with surface loose-textured, with conidial structures arising from the substratum and from aerial mycelia, and with reverse uncolored, pinkish, or in purplish drab shades..... *P. spinulosum* Thom 180
2′. Conidia elliptical to ovate.
aa. Conidia and conidiophore walls roughened, with colonies on malt not developing "sclerotium-like" structures
P. lividum series 189
1″. Colonies deeply lanose, conidiophores 400 to 500μ or more in length, reverse uncolored or in fairly light shades.
aaa. Conidia broadly elliptical to ovate, conspicuously roughened.....*P. lividum* Westling 190
bbb. Conidia narrowly elliptical with ends pointed, delicately roughened
P. aurantio-violaceum Biourge 192
2″. Colonies not deeply lanose, conidiophores comparatively short, reverse in deep violet to violet-black shades, conidia spinulose.....*P. trzebinskii* Zaleski 194
bb. Conidia and conidiophore walls smooth, with colonies on malt agar developing "sclerotium-like" structures
P. turbatum Westling
(in *P. thomii* series)
b. Colonies growing rather restrictedly upon most media, especially Czapek's solution agar.....*P. implicatum* series 196
1′. Conidial areas light blue-green, colony reverse in bright orange-red or red shades, conidia globose to subglobose, in parallel or divergent chains.....*P. multicolor* G.-M. and P. 198
2′. Conidial areas commonly deep blue-green, colony reverse in orange-brown or maroon shades, conidia broadly elliptical, usually in compact columns.....*P. implicatum* Biourge 201
3′. Conidial areas yellow-green to gray-green, reverse in orange-red shades (approaching brick red), conidia strongly elliptical or pyriform.....*P. sublateritium* Biourge 203
2. Colonies appearing velvety or with surface lightly floccose; conidiophores borne primarily as short branches from loosely trailing or compacted vegetative hyphae.....*P. decumbens* series 205
a. Colonies loose-textured, with margin usually thin and generally

consisting of a loose network of interlacing hyphae bearing short conidiophores.

1′. Conidial areas in light gray-green shades with reverse uncolored or in yellow drab shades on Czapek agar but becoming cherry red on malt agar..... *P. chermesinum* Biourge 206

2′. Conidial areas in dull blue-green shades with reverse usually uncolored on all media..... *P. decumbens* Thom 209

b. Colonies close-textured, tough, almost leathery, restricted, with margin compact but showing occasional stolon-like hyphae.

1′. Vegetative mycelium yellow, generally characterizing the colony even in age, sporulating lightly on Czapek agar *P. citreo-viride* Biourge 215

2′. Vegetative mycelium white, often characterizing the colony when young, but developing blue-green conidial areas in one to two weeks, reverse uncolored or in light vinaceous gray shades..... *P. fellutanum* Biourge 212

3′. Vegetative mycelium white to pale vinaceous, sparsely sporulating, reverse bright orange-red to maroon *P. roseo-purpureum* Dierckx 218

3. Colonies floccose with conidiophores arising primarily from aerial hyphae or floccose-funiculose with aerial hyphae collected into ropes or bundles.

a. Colonies predominantly floccose with funiculose character lacking or limited..... *P. restrictum* series 222

1′. Conidia blue-green becoming dull gray, globose, about 2.5μ, conspicuously roughened.. *P. restrictum* Gilman and Abbott 223

2′. Conidia olive-green becoming brown, globose, about 4.0μ, coarsely roughened, tuberculate.. *P. fuscum* (Sopp) n. comb. 226

b. Colonies with funiculose habit predominant or well developed *P. adametzi* series 227

1′. Colonies usually developing dull reddish orange to brown shades in reverse.

aa. Conidia subglobose, 2.0 to 2.5μ, delicately granular *P. adametzi* Zaleski 228

bb. Conidia globose to subglobose, about 3.0μ in diameter, definitely rough..... *P. terlikowskii* Zaleski 231

2′. Colonies quickly developing deep vinaceous to purple colors in reverse and agar..... Vinaceous sub-series 234

aa. Exudate abundantly produced, deep vinaceous, conidiophores short, rarely more than 50μ *P. vinaceum* Gilman and Abbott 234

bb. Exudate lacking or limited, conidiophores longer, 200 to 250μ..... *P. phoeniceum* van Beyma 236

B. Conidiophores mostly branched, occasionally rebranched, each bearing a terminal monoverticillate penicillus but not arranged as a definite apical verticil of metulae (or branchlets)..... Ramigena series 239

1. Colonies growing restrictedly upon all media, mostly 1.5 to 2.5 cm. in diameter in 10 to 12 days.

a. Conidia definitely elliptical, smooth-walled.

1′. Conidial areas in gray-green shades, with conidia strongly ellip-

tical to narrowly cylindrical, with ends broad, not pointed
P. capsulatum Raper and Fennell 242

2′. Conidial areas in blue-green shades with conidia elliptical and with ends somewhat pointed.
P. cyaneum (B. and S.) Biourge 244

b. Conidia globose, ovate, or slightly elliptical and with walls roughened

1′. Conidia globose or nearly so, in divergent chains, not forming columns.....*P. waksmani* Zaleski 246

2′. Conidia ovate to slightly elliptical, in parallel chains forming compact columns.....*P. charlesii* Smith 248

2. Colonies growing more rapidly upon most media, usually 4.0 to 5.0 cm. or more in diameter in 10 to 12 days.

a. Conidia rough, echinulate; colonies vinaceous to reddish brown in reverse.....*P. velutinum* van Beyma 250

b. Conidia smooth; colonies developing yellow in reverse
P. citrinum series
(in the Velutina, pp. 338–354)

Penicillium javanicum Series

Outstanding Characters

Perithecia characteristically produced, at first appearing parenchymatous throughout, often soon becoming sclerotioid, ripening from the center outward, developing asci and ascospores in one to several weeks depending upon the particular species and strain, at maturity showing a definite cellular wall one or more cells in thickness.

Asci borne as short branches from ascogenous hyphae, not in chains, 8-spored. Ascospores lenticular to subglobose, small; with walls smooth or roughened, and (depending upon the species) with equatorial ridges and furrow evident, pronounced, or lacking.

Colonies of most species and strains growing fairly rapidly upon most substrata; characteristically developing abundant perithecia adjacent to the substratum, often appearing granular; with vegetative mycelium developed to a greater or less degree, sometimes enveloping and obscuring the perithecia. Colony surface commonly appearing floccose, seldom velvety.

Penicilli monoverticillate, usually strictly so but occasionally branched, sometimes fragmentary; very sparsely produced in some species and strains, more abundantly in others; usually borne on short branches (conidiophores) from aerial hyphae.

Series Key

(See General Key to Monoverticillata)

The series embraces a group of monoverticillate species which develop perithecia in greater or less abundance. Penicilli are produced rather ir-

regularly and, while typically consisting of small, simple clusters of sterigmata (figs. 36D and 39D), often appear as fragmentary structures without consistent measurements or pattern. The principal unifying structures tying the member-species together are the perithecia which are basically

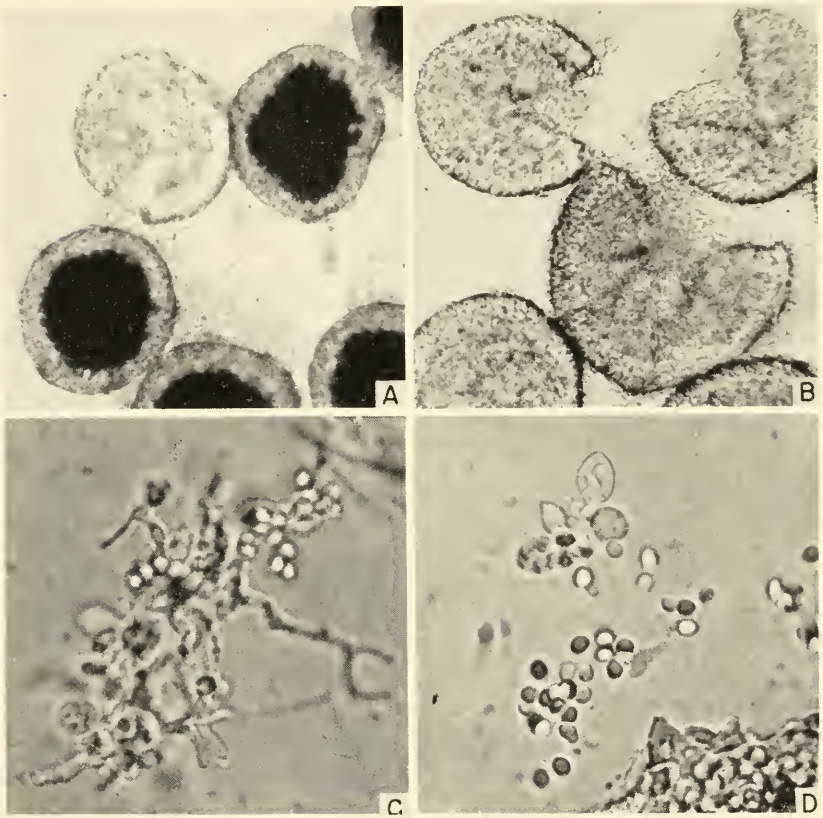


FIG. 35. Ascosporic stage of *Penicillium javanicum* series; *P. javanicum* v. Beyma, NRRL 707, on malt agar at two weeks. *A*, Intact perithecia; dark areas result from air trapped within the perithecia, × 175. *B*, Broken perithecia showing the heavy cellular wall and the fertile ascogenous tissue being squeezed out, × 175. *C*, Small fragment of ascogenous tissue showing scattered asci, × 900. *D*, Asci and ascospores, × 900.

similar in origin, form, texture, and course of maturation in all species (fig. 35). The perithecia arise in the manner described for *Penicillium brefeldianum* by Dodge (1933) and confirmed by Emmons (1935) (see fig. 14). A short branch arises vertically from a hypha at or near the surface of the substratum, and by limited branching produces a loose tree-like network. There is no evidence of sex organs or ascogonial coils at this stage.

Later a knot of rather thick, irregularly wound or clumped hyphae, which represents the beginning of the young ascocarp, or perithecium, appears in a fork of the branching system. Growth is rapid from this stage and the young ascocarp soon consists of a solid mass of pseudoparenchymatous tissue with little or no differentiation except for the somewhat thickened walls of the cells of the outer layers. The ascogenous system apparently occupies a central position. Depending upon the species and strain, and upon the substratum and other environmental conditions as well, asci may begin to appear within 7 to 10 days; or the whole mass may become sclerotioid and ascus formation be delayed for a matter of 3, 4, 5, or more weeks. In some strains and under certain conditions the bodies appear to remain sclerotioid indefinitely and cannot in fact be distinguished from true sclerotia (fig. 13). In any case, wherever asci develop, these first occupy a central position in the perithecium and arise as short branches from the fertile ascogenous hyphae that comprise an enlarging network which gradually disorganizes (digests ?) and replaces the pseudoparenchymatous tissue (fig. 35). Generally speaking, and making certain allowances for some species other than *P. brefeldianum*, Dodge (1933, p. 97) was correct in saying: "The older the ascocarp under good growing conditions the larger the cavity and the greater the number of asci with a corresponding thinning out of the sterile wall layers." In discussing the perithecia of *P. javanicum*, the first described member of the series, van Beyma (1929) reported them to ripen late (usually one month or more) and to consist of a tough pseudoparenchymatous cover, which when broken permitted the fertile hyphae with budding asci to be "pressed out like a skein" (fig. 14E). This phenomenon has been repeatedly observed in our experience. Whereas particular strains and species differ in the relative amounts of this hyphal network and in the proportions of this network to the number of asci produced, it is a characteristic developmental feature of this entire series, and also of the *Carpenteles* series, with biverticillate-asymmetric penicilli, which will be considered later (pp. 260–273).

Five species comprise the series as follows: *Penicillium javanicum* van Beyma, *P. parvum* Raper and Fennell, *P. brefeldianum* Dodge, *P. ehrlichii* Klebahn, and *P. levitum* Raper and Fennell. For convenience, these species may be subdivided into two fairly well defined sub-series.

The first of these sub-series embraces *Penicillium javanicum* and *P. parvum*, and is characterized particularly by colonies that develop abundant red to reddish brown pigmentation upon most substrata. Perithecia are rather late in ripening in both species, particularly the latter, where asci and ascospores commonly do not appear for several weeks. In *P. parvum* colonies are much restricted and ascospores are usually small and show conspicuous equatorial ridges (fig. 37).

The second sub-series, containing *Penicillium brefeldianum*, *P. ehrlichii*, and *P. levitum*, differs from the first by producing colonies with little or no red or reddish pigmentation on any substratum. Perithecia generally ripen earlier, although exceptions are encountered. *Penicillium brefeldianum* is the most abundant and variable member of the series, but in its original and typical aspect is easily recognized from the detailed studies of Dodge (1933) and Emmons (1935). The penicilli developed by this species are generally larger and more characteristic than those of other members of the series (fig. 38). *Penicillium ehrlichii*, as originally described, and in our experience as well, produces very irregular and usually fragmentary penicilli; ascospores are larger than in *P. brefeldianum*, have rougher walls, and show a shallow but definite equatorial furrow (fig. 40). Perithecia are often yellow to light tan or buff, suggesting *P. javanicum* in this regard. *Penicillium levitum* is keyed in the series with *P. brefeldianum*, although we are not too certain of the correctness of such placement. The perithecia closely resemble those of *P. brefeldianum* structurally, but they usually ripen even more quickly, often developing ripe ascospores within a week to 10 days. Ascospores are smooth-walled and show no signs of an equatorial furrow (fig. 41D). The conidial stage is rather unique. Sterigmata are comparatively large, often arise singly on aerial hyphae and seldom occur in clusters of more than 4 or 5 (fig. 42). Conidia are large, smooth-walled, borne in short chains, and the terminal cell is often definitely enlarged. The conidial stage is strongly suggestive of structures seen in the genus *Monascus*.

The different species comprising the series may be separated as shown in the initial portion of the above key to the Monoverticillata.

Penicillium javanicum van Beijma,[1] in Verhandel. Kon. Akad. Wetensch. Amsterdam Afd. Nat. (Tweede Sectie) **26** (4): 16–19, 3 figs. 1929; Lockwood *et al.*, Zentbl. f. Bakt. etc., (II) **90:** 412–413, fig. 1. 1934; Emmons, Mycologia **27:** 145–146, figs. 12 and 16. 1935.

Synonym: *Carpenteles javanicum* (van Beijma) Shear, in Mycologia **26:** 107. 1934.

Colonies on Czapek's solution agar (Col. Pl. III) growing fairly rapidly, 3.5 to 4.0 cm. in 12 to 14 days at room temperature, comparatively thin, surface appearing lightly floccose, conspicuously furrowed in a predominantly radial pattern with central area often more or less raised (fig. 36A), in color showing gradual gradation from yellowish shades near olive-buff (Ridgway, Pl. XL) at the colony margin to dull yellow-orange shades near vinaceous fawn or fawn (R., Pl. XL) in colony centers; conidial structures

[1] In later publications the name appears as van Beyma, rather than van Beijma, and it is generally cited in that manner.

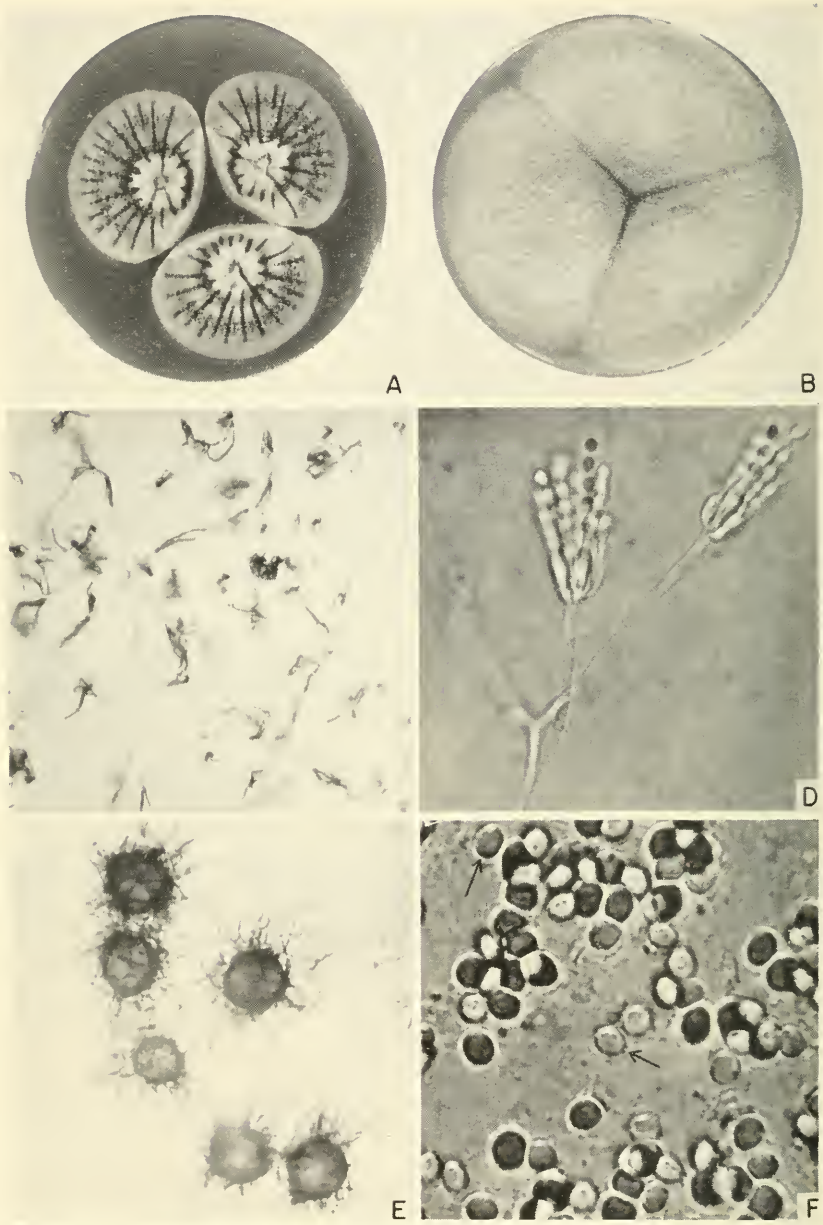


FIG. 36. *Penicillium javanicum* v. Beyma, NRRL 707. *A*, Colonies on Czapek agar at two weeks. *B*, The same on malt agar; note granular effect produced by perithecia in inter-colony areas. *C*, Low-power view of penicilli on hay agar, × 100. *D*, Detail of characteristic penicilli, × 900. *E*, Low-power view of perithecia, × 100. *F*, Ascospores, × 1500; note equatorial furrow on spores indicated by arrows.

PLATE III

TOP: Penicillium javanicum van Beyma, NRRL 707, on Czapek's solution agar, 10 days. *CENTER: Penicillium sclerotiorum* van Beyma, NRRL 2074, on steep agar, 12 days. *BOTTOM: Penicillium frequentans* Westling, NRRL 1915, on Czapek's solution agar, 10 days. (Color photographs by Haines, Northern Regional Research Laboratory. Reproduced through co-operation of Chas. Pfizer & Co., Inc.)

minute, limited in number, not influencing the colony appearance; perithecia abundantly produced and lending a slightly granular appearance to the thin, intercolony margins, borne adjacent to the substratum, regularly enmeshed in and overgrown by a loose aerial mycelium, not superficially evident in deeper colony areas; exudate abundantly produced in most strains, approximately vinaceous fawn in color, sometimes dominating the central colony area; odor lacking or indefinite; reverse becoming strongly colored, at first in dull yellow or greenish brown to reddish shades, in age becoming deep brown to maroon; penicilli strictly monoverticillate, few in number, very small, bearing few and divergent chains of conidia up to 100μ or more in length (fig. 36C); conidiophores arising mostly as branches from aerial hyphae, 100μ or less in length, occasionally from submerged hyphae 150 to 200μ by 2.2 to 2.8μ, seldom branched, with walls smooth; sterigmata borne in groups of 2 to 6, usually 3 or 4, measuring 8 to 10μ by 2.0 to 2.5μ with long, narrow conidium-bearing tubes; conidia elliptical to subglobose, mostly about 2.5μ in long axis (fig. 36D). Perithecia abundantly produced, oblong to globose (fig. 36E), occasionally somewhat angular, mostly 100μ or less in diameter, at first consisting of heavy-walled parenchyma-like cells throughout, ripening late, usually developing asci and ascospores after two to three weeks; asci borne as lateral buds from fertile hyphae (fig. 35D), globose to oblong when ripe, about 6 to 8μ in diameter, 8-spored; ascospores heavy walled, showing limited surface irregularities and a trace of an equatorial furrow, lenticular, about 2.5 to 3.0μ by 2.0 to 2.5μ (fig. 36F).

Colonies on steep agar like the above in general pattern and texture but growing more rapidly, 5 to 5.5 cm. in 2 weeks, exudate lacking or limited in most strains, quickly developing deep red-brown to maroon shades in reverse; penicilli as on Czapek; perithecia abundantly produced, as described above.

Colonies on malt agar spreading broadly, up to 5.5 to 6.0 cm. in 2 weeks, plane, thin, in dull shades near olive-buff (R., Pl. XL), consisting of a dense, uniform layer of perithecia adjacent to the substratum (fig. 36B), overgrown but not obscured by a loose network of aerial hyphae; penicilli slightly larger than on Czapek and borne on conidiophores up to 300μ in length. Perithecia ripening more rapidly than above, developing asci and ascospores in about 12 days.

Colonies on hay agar spreading broadly, very thin, producing fewer perithecia and relatively more conidial structures than on the above media; reverse uncolored except deep red in limited central area. Perithecia ripening within 8 to 10 days and showing abundant free ascospores in 12 to 14 days.

Colonies on cornmeal agar spreading broadly with vegetative mycelium largely submerged, producing abundant perithecia in a thin layer on the

agar surface, ripening quickly in most strains; reverse ranging from colorless or nearly so in some strains through yellow-orange to definitely red in others; ascospores as described above.

Species description centered upon van Beyma's type isolated from tea roots in Buitenzorg, Java, and now maintained in our collection as NRRL 707. A strain, presumably type, received in May 1946, from the Centraalbureau as *Carpentelcs javanicum* (v. Beyma) Shear differs only in producing smaller perithecia-like structures and in its failure to develop ascospores within four weeks. The species is represented by numerous additional strains isolated at this laboratory from soil samples collected in sub-tropical areas including Brazil, Central America, India, and Northern Argentina. Among these latter may be listed: NRRL 2078, isolated in December 1945 from a sample of soil contributed by Dr. O. G. Lima, Recife, Brazil; and NRRL 2079 isolated from a sample of soil sent to us by Dr. B. B. Mundkur, New Delhi, India. A second strain received from the Centraalbureau in May 1946, as an isolate of *Carpenteles javanicum* from "Toba" heather, represents a member of the *Penicillium javanicum* series but more nearly approximates *P. brefeldianum* Dodge.

In our experience conidia and sterigmata average a little smaller than van Beyma's and asci are regularly 8-spored rather than 4- to 6-spored as noted by him. He did not report any irregularities in the spore surface nor give any indication of an equatorial line or furrow. Otherwise the description as presented above is in satisfactory agreement with the original species diagnosis published by van Beyma in 1929.

Penicillium parvum Raper and Fennell, in Mycologia **40**: 508–511, fig. 1. 1948.

Colonies on Czapek's solution agar growing very restrictedly, attaining a diameter of 1.5 to 2.0 cm. in two weeks and 3 to 4 cm. in four to five weeks, raised 1 to 2 mm., sometimes folded or wrinkled (fig. 37A), consisting of a very tough close-textured mycelial felt with surface consisting of a thin growth of fine aerial hyphae appearing somewhat floccose, mostly in white through flesh to dull yellow shades, becoming deeper and somewhat vinaceous in age, penicilli usually lacking (see description on hay agar); incipient perithecia (appearing as semi-sclerotioid masses of thick-walled parenchyma-like cells) developing within two to three weeks, spherical to oblong or slightly angular, yellow in color, buried deep in the mycelial felt, failing to produce asci and ascospores even within four to five weeks (see hay agar below); exudate usually abundant in rich brown shades becoming deep purple-brown in age; odor lacking or indistinct; reverse at first in vinaceous fawn shades becoming deep maroon in age.

Colonies on steep agar restricted but growing more rapidly thar above,

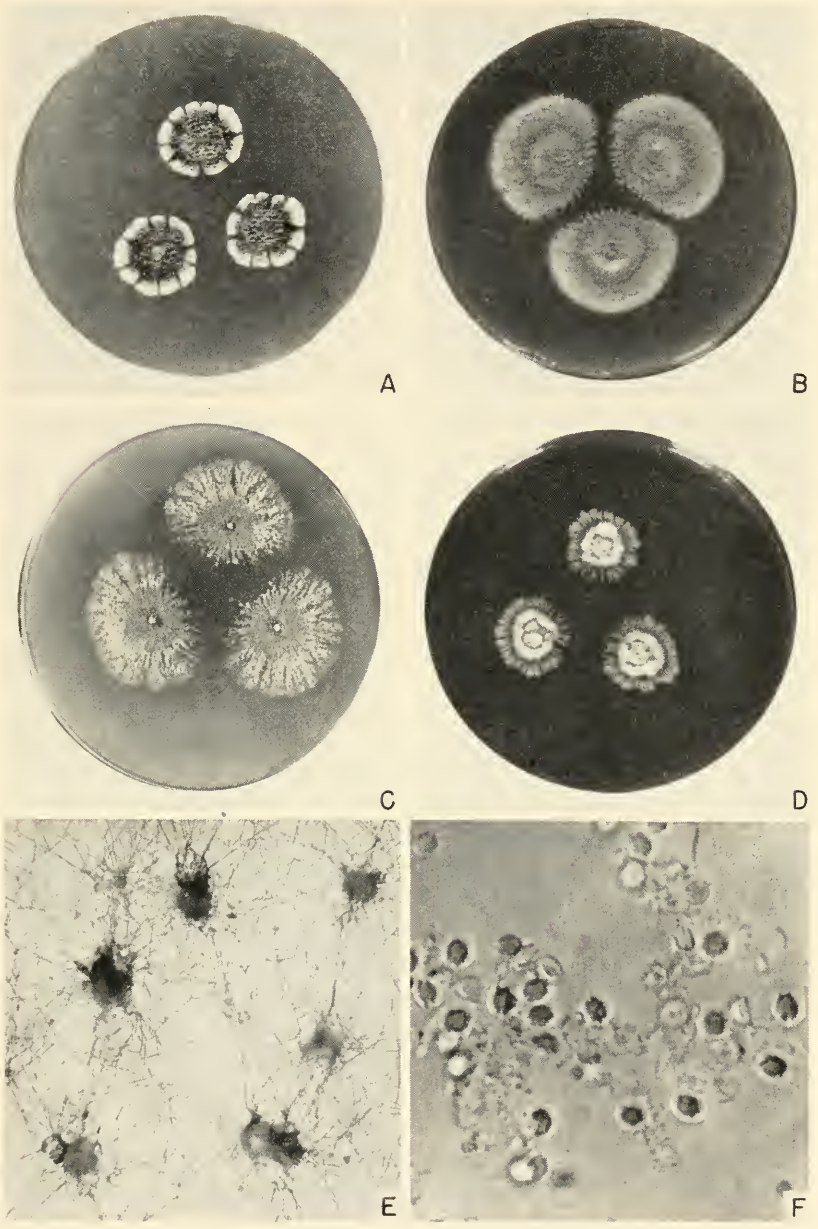


FIG. 37. *Penicillium parvum* Raper and Fennell, NRRL 2095. *A*, *B*, *C*, and *D*, Two-week-old colonies on Czapek, malt, corn meal, and hay agars respectively. *E*, Low-power view of perithecia on corn meal agar, × 60. *F*, Ascospores, × 1500; note prominent ridges and equatorial furrows.

2.0 to 2.5 cm. in two weeks, in texture and appearance essentially as on Czapek but with surface looser textured and deeper; exudate more abundant, deep maroon; penicilli usually lacking; not developing asci and ascospores within one month.

Colonies on malt agar about 1.5 to 2.0 cm. in two weeks, 0.5 to 1.0 mm. deep, plane or nearly so, consisting of a dense layer of perithecia adjacent to the agar surface (fig. 37B), commonly overgrown by a thin, loose network of orange to light brown aerial hyphae, lending to the colony its characteristic texture and color; penicilli very few in number, strictly monoverticillate, on short branches from submerged or trailng hyphae, not affecting the colony appearance; no exudate or odor; reverse in dull brown shades.

Colonies on hay infusion agar restricted, about 2.5 to 3.0 cm. in three to four weeks, very thin, vegetative mycelium largely submerged, producing numerous perithecia in an uneven layer at the agar surface to give a granular effect (fig. 37D), in tan to brown shades; penicilli very few in number, developing primarily at the colony margins in old plates, strictly monoverticillate, borne on short branches from submerged or trailing hyphae; conidiophores short, usually 50μ or less and commonly 25 to 40μ in length by about 1.5μ in diameter, smooth-walled, bearing small penicilli consisting of verticils of 3 to 6 parallel sterigmata; sterigmata mostly 7 or 8μ by 1.2 to 1.5μ with conidium-bearing tips slightly narrowed; conidia at first definitely elliptical, about 1.5 to 2.0μ by 1.2 to 1.5μ, in age becoming almost subglobose, mostly 1.5 to 1.8μ in diameter, smooth-walled, adhering in fairly long chains in fluid mounts. Perithecia spherical to oblong, mostly 100μ or less in diameter (fig. 37E), occasionally up to 150μ, surrounded by very thin wefts of sterile hyphae, at first tending to be sclerotioid and of uniform texture throughout, consisting of heavy-walled parenchyma-like cells, ripening late from the center outward, beginning to develop asci and ascospores in three to four weeks, at two months filling the perithecium except for an outer wall 2 to 3 cells thick; asci apparently borne as lateral branches from fertile hyphae, chains not seen, round to oval in outline, about 6 to 7μ at maturity, 8-spored; ascospores lenticular, very small, 2.0 to 2.4μ by 1.5 to 1.8μ, with walls definitely roughened and with two prominent equatorial ridges rather widely separated to give a definite pulley-like appearance (fig. 37F).

Colonies on cornmeal agar spreading slowly, 5 to 6 cm. in four weeks, very thin, vegetative mycelium submerged; perithecia produced abundantly along radiating dendroid lines (fig. 37C), almost naked but surrounded by very sparse hyphal networks to give a conspicuously granular appearance to the colony, perithecia developing and ripening as on hay agar; penicilli usually absent.

Species description based upon NRRL 2095 as type, isolated in July 1945 from a sample of soil from Nicaragua contributed by Dr. A. G. Kevorkian.

The binomial, *Penicillium parvum*, was selected because of the minute character of the penicilli, conidia, and ascospores. *Penicillium minutum* would have constituted a more suitable name, but the describers refrained from adopting this because of Bainier's prior use of the name *Citromyces minutus* (Bul. Soc. Myc. France **29:** 137–144, Pl. IV, fig. 3. 1913) for an apparently strictly conidial form.

Penicillium parvum is believed to be more nearly related to *P. javanicum* van Beyma than to any other described species. It resembles the latter in producing colonies marked by a rich reddish brown pigmentation in reverse; in showing strictly monoverticillate penicilii borne on short branches; and in developing perithecia, at first sclerotioid in character, which subsequently ripen from the center outward. It differs from this species in its more restricted growth upon all media, particularly upon Czapek's solution agar; in the smaller dimensions of conidial structures and parts of the same; in the more delayed ripening of its perithecia; and, particularly, in the character of its ascospores. These are consistently smaller, more conspicuously roughened, and show more strongly developed equatorial ridges and furrows. The species is represented, at present, by a single strain, which at one time was considered merely as an extreme variant of *P. javanicum*. However, differences in rate of growth and details of morphology, between this culture and typical strains of *P. javanicum*, seemed to warrant recognition of a new species.

Penicillium parvum is apparently favored by a culture substrate of high osmotic tension. It grows better upon all substrata as these dry out in the culture plate or tube, producing conidial structures on most media only in marginal areas of aging cultures. The production of penicilli upon sporulation agar to which a high concentration of NaCl has been added affords additional evidence. Growth of the fungus upon Czapek's solution agar is increased when the sugar concentration is raised to 20 per cent.

Penicillium brefeldianum Dodge, in Mycologia **25:** 90–104, figs. 1 and 2, Pls. 18 and 19. 1933; see also Emmons, in Mycologia **27:** 145, figs. 13a and b. 1935

Synonym: *Carpenteles brefeldianum* (Dodge) Shear, in Mycologia **26:** 107. 1934.

Species diagnosis *fide* Dodge (fig. 38):

"Mycelium and conidial masses variously colored depending first on the particular race and second on the nature of the culture medium, whitish, cream, peach, fawn,

mouse or grayish to pale green; on corn meal agar sparse with few conidia; homothallic.

"Conidia spherical to short elliptical, smooth, 1.5–2 x 2–3μ; penicillus commonly monoverticillate; sterigmata 2.5–3 x 7–10μ, the spore-forming tube prominent; conidiophore short, slightly enlarged at the tip, side branches rather frequent, 3–4 x 5–150μ.

"Ascocarps spherical, whitish to pale tan, non-ostiolate, superficial, growing upon, and more or less surrounded by a loose weft or network of hyphal branches, 100–200μ in diameter, mostly about 150μ; asci oval, pear-shaped to spherical, 7.5–12 x

FIG. 38. *Penicillium brefeldianum* Dodge. *a–d*, Various stages in the development of the conidial stage; *e* and e_1, Spherical and oval asci; *f* and f_1, Spherical and elliptical ascospores; *g–i*, Three types of ascospore germination, *g* showing fragments of the spore wall clinging to the germ vesicle as figured by Brefeld. (After Dodge, Mycologia, *25*. 1933.)

10–15μ, 8-spored; ascospores globose to slightly elliptical, hyaline, finely echinulate, 2.5–3.8 x 3–4μ.

"Isolated from alimentary tract of human."

Dodge's description and figure are inserted since these adequately present the species in question. The type strain, received from Dodge in 1932, and continued in artificial culture since that time has become predominantly conidial, and upon many substrata now fails to develop any perithecia. On vegetable extract media, including hay infusion, malt and corn-meal agars, this strain, now maintained as NRRL 710, still produces small rounded sclerotioid bodies, rarely more than 50μ in diameter, some of which

very tardily (4 to 5 weeks) develop mature asci and ascospores in limited numbers.

Ripening of the ascocarp, or perithecium, apparently follows the course reported by Dodge (1933). Perithecia were described as at first consisting of "a solid mass of pseudoparenchymatous tissue with little or no differentiation except for the somewhat thicker walls of the cells of the outer layer." The ascogenous system occupied a central position and gradually increased by disorganization of the surrounding tissue. In old perithecia the entire body, with the exception of a comparatively thin outer wall, was composed of mature asci. The fruit body was reported not to be hard and stone-like at any stage although some structures more definitely sclerotioid than most were encountered. In certain cultures, asci were visible in 7 days and ascospores were matured within 10 days after the cultures were planted; in other cultures the process was more delayed. Ascospores were reported as finely echinulate but no mention was made of an equatorial band or furrow, nor was such shown in his illustrations. Ascospores germinated usually by splitting, with the spore walls remaining in two fragments as in definite bi-valve types. Emmons (1935) figured the ascospore with a faint suggestion of an equatorial furrow. In our experience such a line or furrow is sometimes evident although usually lacking.

The conidial apparatus in NRRL 710 remains typical of the species. The penicilli are typically monoverticillate but not infrequently show branched structures as originally illustrated. Sterigmata consistently show the narrow conidium-bearing tip described by Dodge. Conidia are definitely elliptical and agree satisfactorily with his original measurements (fig. 39C and D).

Although the species was shown to be homothallic by both Dodge (1933) and Emmons (1935), most strains of *Penicillium brefeldianum* in continued artificial culture show a marked tendency to develop sectors that are predominantly conidial. Even by exercising special care as to areas from which recultivations are made, it is often extremely difficult to maintain a strain which produces abundant and normally maturing perithecia. Strains freshly isolated from nature generally produce quantities of perithecia, but often lose this capacity in large measure after relatively few transfers. The type, NRRL 710, is an example. Other strains maintained in this laboratory for more than a decade show no evidence of developing asci, although there remains some suggestion of perithecial initials. A strain received from the Centraalbureau in February 1946, as *Carpenteles brefeldianum* (Dodge) Shear, undoubtedly ascosporic when first isolated and diagnosed by them, produces small rounded masses of heavy-walled cells but shows no evidence of ascospore development.

A number of strains believed to represent *Penicillium brefeldianum* Dodge

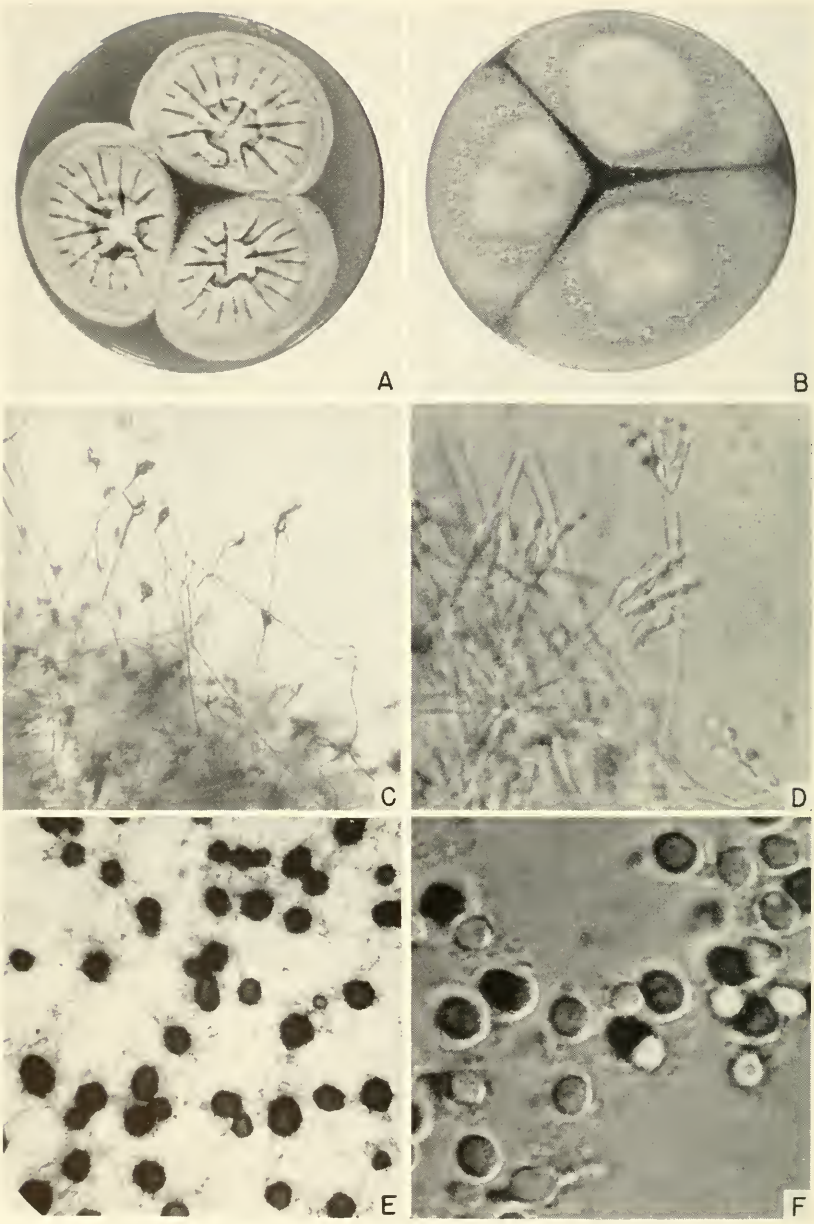


FIG. 39. *Penicillium brefeldianum* Dodge, NRRL 2083. *A* and *B*, Two-week-old colonies on Czapek and malt agars. *C*, Low-power view of penicilli on malt agar × 100; *D*, Detail of delicate penicilli characteristic of species, × 900. *E*, Low-power view of perithecia, × 40. *F*, Ascospores, × 1500; note delicately spinulose walls.

have been examined in our current study. One of these, NRRL 2083, received in November 1946, from Wm. I. Illman, University of Toronto, apparently duplicates the original type almost exactly. Perithecia are produced in great numbers and these average about 150μ as reported by Dodge. They are light tan in color and are rounded to oblong. Perithecia ripen quickly and are often filled with mature ascospores within two weeks. The ascospores agree closely with the species description in form and dimensions (fig. 39F), and in comparative mounts are indistinguishable from the few still produced by the type, NRRL 710. The conidial apparatus likewise duplicates Dodge's original figures and description. Since Dodge did not include detailed colony descriptions in his diagnosis, these are presented for NRRL 2083:

Colonies on Czapek's solution agar attaining a diameter of 3 to 4 cm. in two weeks, radially furrowed with central area commonly raised, consisting of a comparatively thin basal felt with surface loosely floccose (fig. 39A), mostly in white to light yellow shades, usually light sporing, conidial structures borne largely from the aerial mycelium, commonly not affecting the colony appearance but sometimes abundantly produced in localized sectors; perithecia numerous, often developing after ten days to two weeks, usually in a layer adjacent to the agar surface, commonly obscured by the overlying vegetative growth, occasionally appearing massed in sectors predominantly perithecial, spherical to oblong, from 100 to 200μ in diameter (fig. 39E), flesh to light tan (sandy) in color; exudate limited, clear; odor lacking or indefinite; reverse in bright to dull yellow shades becoming brown in age.

Colonies on steep agar as above but growing more rapidly, 5.0 to 5.5 cm. in two weeks, somewhat zonate, heavier sporing with conidial areas in dull gray-green shades, perithecia developing as above but more abundantly.

Colonies on malt agar spreading broadly, about 6 cm. in diameter, generally plane, appearing definitely granular to the unaided eye (fig. 39B), but with central area floccose and comparatively heavy-sporing; perithecia very numerous, in a dense layer at the agar surface, in form and dimensions as described above, when massed lending to the colony a flesh to avellaneous (Ridgway, Pl. XL) color, developing abundant ripe ascospores in 10 to 12 days.

Penicillium brefeldianum should be regarded as comprising a variable series of strains obviously interrelated but showing considerable individuality. NRRL 2091, isolated from Nicaragua soil in October 1945, essentially duplicates NRRL 2083 as described above; NRRL 2092, isolated from a sample of soil from Johannesburg, South Africa, in November 1945, differs primarily in producing ascospores more coarsely roughened as in *P. chrlichii* but without the conspicuous equatorial furrows seen in that species; and NRRL 2093, isolated from a sample of soil from Sao Paulo,

Brazil, in June 1944, differs principally in producing ascospores with walls almost smooth and usually without a trace of furrow, and perithecia in yellow rather than flesh to sandy shades.

Occasional strains appear intermediate between *Penicillium brefeldianum* and members of the *Carpenteles* series such as *P. egyptiacum* van Beyma. NRRL 2094 is representative. This culture produces perithecia in great abundance. These are of the type seen in *P. brefeldianum* and ripen usually within 10 to 12 days, and the ascospores are almost indistinguishable from those of *P. brefeldianum*, NRRL 710 and 2083. They are delicately roughened over the whole surface and seldom show a definite equatorial line, although on some spores the echinulations are so arranged as to suggest about four faint longitudinal lines. The conidial apparatus is markedly different from typical *P. brefeldianum* strains. Penicilli are typically biverticillate-asymmetric. In this respect it is strongly suggestive of members of the *Carpenteles* series, particularly *P. egyptiacum* van Beyma. Although NRRL 2094 appears to be intermediate between the above mentioned species, we refrain from assigning it with either, or from describing it as new. The continued isolation and examination of new strains may later indicate the need for recognition of a new species intermediate between the *P. javanicum* and the *Carpenteles* series as now considered. On the other hand, further study may definitely establish the unity of the two series without regard for the form of the conidial apparatus developed.

Penicillium ehrlichii Klebahn, in Ber. deut. bot. Gesell. **48:** 374–389, figs. 1–14. 1930; see also, Emmons, in Mycologia **27:** 145, figs. 14 and 16. 1935.

Colonies on Czapek's solution agar growing restrictedly, attaining a diameter of 1.5 to 2.0 cm. in 2 weeks at room temperature, with margin irregularly dissected from the uneven growth of the vegetative mycelium (fig. 40A), often largely submerged, with surface growth first appearing as localized aerial tufts near the colony margin but becoming continuous in older central areas and consisting primarily of loosely interwoven aerial hyphae surrounding and more or less obscuring the abundantly developing perithecia, colonies white to pale yellow near ivory yellow to colonial buff (Ridgway, Pl. XXX); conidial structures very limited in number, not influencing the colony appearance; no exudate produced; odor lacking; reverse uncolored or in yellow shades; penicilli few in number, very irregular in pattern, commonly appearing fragmentary, consisting of limited numbers of irregularly arranged sterigmatic cells bearing short chains of conidia; sterigmata rarely occurring as true verticils, often borne singly or in groups of 2, 3, or occasionally more, strongly divergent and usually arising at different levels, variable in form and dimensions, commonly 10 to 15μ by

2.5 to 3.5μ with conidium-bearing tips comparatively long and definitely narrowed; conidia mostly elliptical, 4.0 to 5.0μ by 3.5 to 4.0μ, with ends often more or less pointed, smooth-walled. Perithecia abundantly produced, globose to oblong up to 150 to 200μ in diameter (fig. 40C), ripening

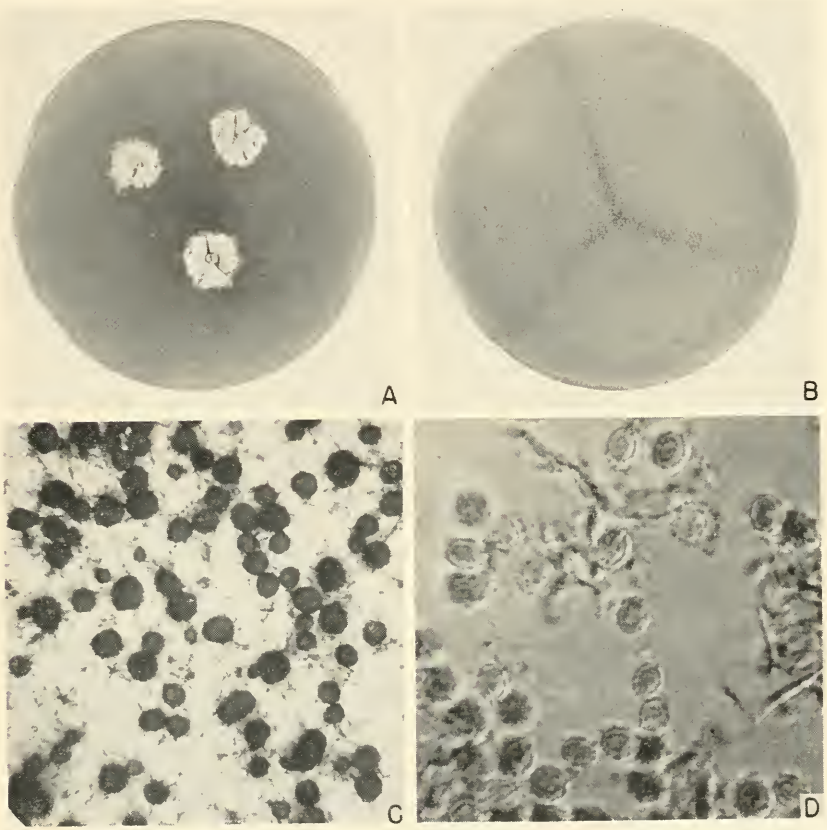


FIG. 40. *Penicillium ehrlichii* Klebahn, NRRL 708. *A* and *B*, Two-week-old colonies on Czapek and malt agars. *C*, Low-power view of perithecia, × 40. *D*, Ascospores, × 1500; note conspicuously roughened walls and equatorial furrows in occasional spores that are properly oriented.

slowly, at 2 weeks composed throughout of pseudoparenchymatous tissue, developing asci and ascospores after 15 to 20 days; asci borne as lateral branches from fertile hyphae, spherical to oblong when ripe, 8 to 10μ in diameter, 8-spored, ascospores lenticular, 3.5 to 4.0μ by 3.0 to 3.5μ, with walls conspicuously spinulose and showing a shallow equatorial furrow and low marginal crests (fig. 40D.).

Colonies on steep agar spreading broadly, attaining diameters up to 8 cm.

in 2 weeks at room temperature; plane or nearly so, typically consisting of a dense layer of perithecia enmeshed in a limited non-flocculent network of sterile hyphae, with colony surface finely but conspicuously granular in orange-yellow shades near cinnamon-buff through clay color to tawny olive (R., Pl. XXIX) occasionally showing pinkish tints; no exudate produced; odor lacking; reverse in deep orange-red shades; penicilli few in number, fragmentary; perithecia as described above, developing abundant ripe asci and ascospores in 12 to 14 days.

Colonies on malt agar spreading broadly, plane, consisting of a fairly close, thin layer of perithecia enmeshed in a loose network of sterile hyphae (fig. 40B); colonies appearing conspicuously granular, from ivory yellow to deep colonial buff (R., Pl. XXX), in some strains tending to produce conspicuous sectors differing in the relative abundance of perithecia and vegetative growth; penicilli very fragmentary, limited in number; perithecia ripening quickly, producing abundant asci within 10 to 12 days.

Colonies on hay agar spreading, 5.0 to 6.0 cm. in 2 weeks, very thin, growing irregularly, producing abundant perithecia; conidial structures scattered but usually more abundant than on the above media, very irregular in pattern with elements as described on Czapek; perithecia ripening quickly with mature asci and ascospores in 8 to 10 days.

Species description based upon Klebahn's type received from him in July 1931 and now maintained as NRRL 708. This culture had been isolated originally by Professor F. Ehrlich, Breslau, and was reported to produce a strong pectin-dissolving enzyme. The species is also represented by NRRL 709 obtained from the Thom Collection as No. 5409. A culture received from the Centraalbureau as Klebahn's type, hence duplicating NRRL 708 in origin, differs from the latter only in producing colonies which tend to develop sectors characterized by less abundant perithecial development. Measurements obtained in our observation, as recorded above, are in almost complete agreement with Klebahn's original species diagnosis. The strains of *Penicillium ehrlichii* in our possession appear to suffer from some nutrient deficiency since they grow very restrictedly upon Czapek's solution agar containing sucrose, nitrate, and other mineral salts but grow luxuriantly upon media such as steep, malt, and hay agars which contain extracts of natural products.

Penicillium levitum Raper and Fennell, in Mycologia **40**: 511–515, fig. 2. 1948.

Colonies on Czapek's solution agar growing rather restrictedly, about 3.0 to 4.0 cm. in 2 to 3 weeks at room temperature, comparatively thin, consisting of a close felt, tearing with difficulty, central area raised, pulling away from the culture dish and usually splitting along deep radial furrows

(fig. 41A), surface appearing almost velvety but consisting of a thin network of short, closely interwoven vegetative hyphae, white but gradually developing light buff to flesh shades in marginal areas, in age sometimes showing even yellow and lilac zones, conidia limited, borne on very reduced fruiting structures (see 20 per cent sugar-Czapek) commonly consisting of

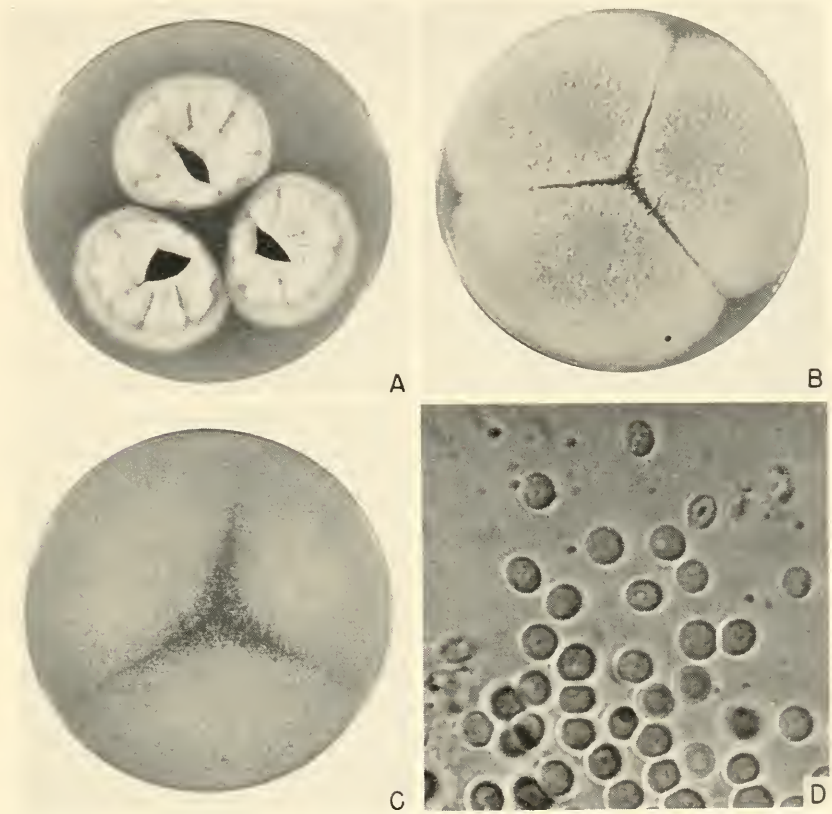


FIG. 41. *Penicillium levitum* Raper and Fennell, NRRL 705. *A*, *B*, and *C*, Colonies on Czapek, malt, and corn meal agars, respectively. *D*, Ascospores, × 1500; note smooth walls. See also fig. 14 showing ascosporic stage of this species.

single sterigmatic cells, not influencing the colony appearance; perithecial primordia present in limited numbers (see malt agar below), buried in the mycelial felt, not developing mature asci or ascospores and not affecting the colony appearance; exudate limited, clear; odor lacking; reverse in yellow shades from citrine to dull buff.

Colonies on Czapek's solution agar containing 20 per cent sucrose as described above but developing conidial structures (fig. 42A) and perithecial

initials more abundantly; conidiophores arising as short branches from aerial hyphae, smooth-walled, mostly 20 to 35μ by 2.0 to 2.8μ, often shorter and rarely longer than 50 or 60μ; penicilli consistently small, simple; sterigmata rarely more than 4 or 5 in the verticil, commonly irregularly arranged, often occurring in pairs or singly, variable in size, mostly 7 to 12μ by 2.2 to 3.3μ when borne in clusters, up to 20 to 25μ by 3.0 to 3.5μ when arising singly, showing some tendency to be wedge-shaped but narrowing abruptly to conspicuous conidium bearing tubes; conidia globose to subglobose, oval or somewhat pyriform with comparatively heavy, smooth walls, varying greatly in dimensions (fig. 42A), mostly 4.0 to 6.0μ in diameter but ranging from 3.0 to 8.0μ, borne in very short divergent chains, consistently larger in some chains than in others and with terminal conidia generally larger than younger conidia in the same chain.

Colonies on steep agar growing as on Czapek but less deeply furrowed and producing abundant perithecia largely near the colony surface, ripening within 10 days to 2 weeks.

Colonies on malt agar spreading broadly, attaining a diameter of 6 cm. in 2 to 3 weeks, plane, occasionally zonate (fig. 41B), growing margin 0.5 to 1.0 cm. wide, white to light flesh colored, central area in shades near avellaneous from the abundant perithecia borne in a loose mycelial felt; conidial structures lacking or very limited in number; perithecia spherical or nearly so, mostly 50 to 100μ in diameter (fig. 42B), in light tan shades, at first consisting of parenchyma-like cells throughout but quickly developing fertile tissue in central areas; asci evident within 4 to 5 days and ascospores beginning to ripen within a week, fertile area progressing outward and within 10 days to 2 weeks filling the entire perithecium except for a thin peridium, one to two cells thick; asci borne as short branches from fertile hyphae (fig. 42C), not in chains, spherical to oval or oblong, 8 to 10μ in diameter when mature, 8-spored; ascospores smooth, polished, broadly elliptical to subglobose, 3.5 to 4.5μ by 3.0 to 4.0μ, comparatively heavy-walled, without any indication of equatorial furrow or ridges (fig. 41D).

Colonies on cornmeal agar spreading broadly, up to 6 cm. in 2 to 3 weeks, very thin, vegetative mycelium submerged or forming a loose network at the agar surface; perithecia rather sparsely produced—in form, dimensions, and development as on malt agar; conidial stage lacking or very limited.

Species description based upon NRRL 705 received without name by Thom in 1936 from Dr. B. O. Dodge as an isolate from modeling clay. This culture has been maintained in our collection since that date as an unidentified member of the general series with *Penicillium brefeldianum*. Careful examination of this culture, during our current study and detailed comparison with described species leads us to regard the form as new. The binomial, *P. levitum*, from the Latin *lēvitas* (smoothness), is applied

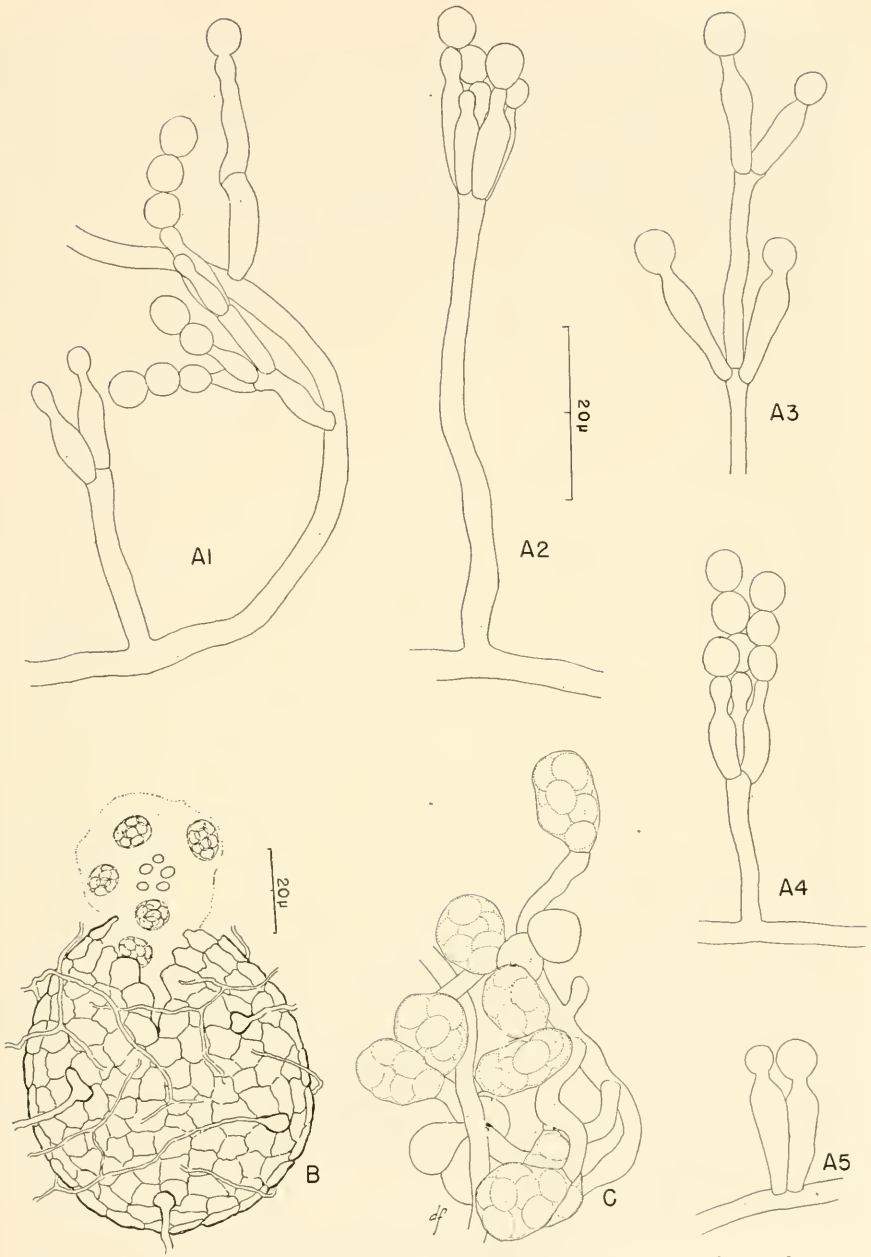


FIG. 42. *Penicillium levitum* Raper and Fennell. A_1–A_5, Diminutive and apparently fragmentary penicilli characteristic of this species. *B*, Perithecium partially crushed indicating the manner in which asci and ascospores are expelled. *C*, Asci borne terminally upon short branches from fertile hyphae.

because of the conspicuously smooth character of all walls, especially of conidia and ascospores.

Upon most substrata, and particularly those containing vegetable extracts, the stock strain of *Penicillium levitum* produces abundant perithecia but very few sterigmatic cells, either grouped as simple penicilli or arising singly from aerial hyphae. Sector variants characterized by increased conidium formation and an absence of perithecia are occasionally observed, and sub-cultures derived from them seem to maintain the characteristics of the sectors. Conidia are produced fairly abundantly and upon some substrata, *e.g.*, 20 per cent sugar-Czapek, the colony surface may assume a light, pale blue-gray tint. While the number of conidia produced in such variant sub-strains is much greater than in the stock, the penicilli produced are not more complex and seldom show clusters of more than 4 or 5 sterigmata. Measurements of conidia and sterigmatic cells remain unchanged.

The perithecia of *Penicillium levitum* are less highly specialized than the initially sclerotioid structures which characterize most other members of the *P. javanicum* series. Conidial structures also differ from other members of the series. Whereas 4 or 5 sterigmata may be arranged in a simple verticil, meeting the essential requirement for placement in the genus *Penicillium*, such definite structures are not consistently produced and the total conidial picture is strongly suggestive of the genus *Monascus*. Such relationship is further suggested by the fact that ascus walls break down rather quickly, leaving the spores free within the ripening perithecium. The species is regarded as properly assignable in the genus *Penicillium* but somewhat transitional in the direction of *Monascus*.

Perithecia of *Penicillium levitum* ripen more rapidly than those of other species belonging to the *P. javanicum* series but apparently follow the same basic pattern of development (fig. 14). The young perithecium rapidly assumes its ultimate size and appears parenchymatous throughout. A mass of fertile tissue soon develops in the central area and asci may appear as early as the 4th or 5th day in contrast to two or more weeks in such species as *P. javanicum* and *P. parvum*. The mass of asci and ascospores usually fills the perithecium within two weeks or less and a thin peridium 1 or 2 cells thick confines the ascospores at maturity (fig. 42B). The perithecium is hardly firm at any stage and is certainly not sclerotioid, but the continuity of parenchyma-like tissue when young, and the presence of a definite continuous wall at maturity unquestionably place it in the *P. javanicum* series.

OCCURRENCE AND SIGNIFICANCE

Members of the *Penicillium javanicum* series represent soil forms primarily, although they may occur in other substrata including vegetable

materials undergoing slow decomposition or manufactured items rich in starch or other plant products. Nowhere do they appear in great abundance, and it is doubtful whether they exert any substantial effect upon decomposition processes in nature.

Penicillum javanicum van Beyma is capable of producing substantial amounts of fat under proper conditions of culture, and it was studied rather exhaustively from this point of view by a research group in the Bureau of Chemistry headed by Herrick and May. Lockwood (1933) and Lockwood, *et al.* (1934) reported maximum quantities of fat (up to 34.6%) in mycelia produced upon media containing sugar concentrations of approximately 30 per cent; a higher ratio of fat to total weight of mycelium occurred in media containing 40 per cent glucose, but the amount of mycelium developed was markedly reduced. Optimum salt concentrations were investigated and NH_4NO_3 was found to be the most suitable source of nitrogen. The fermentation was most efficient when conducted in shallow, surface cultures. Increased air pressure was deleterious. The mold was found to produce some citric acid from glucose, sucrose, and xylose. Sodium oxalate was produced from the sodium salts of gluconic, citric, acetic, malic, fumaric, succinic, and tartaric acids. Ward, *et al.* (1935) subsequently reported the successful employment of shallow aluminum pans for carrying out this fermentation. They found the free acid content of the fat obtained from mycelium grown upon 30 to 40 per cent glucose solutions to be much higher than that of fat similarly derived from 20 per cent glucose solutions upon which the mold made its maximum growth. In addition to fat, the mycelium yielded a complex carbohydrate and a chitinous substance. The composition of the fat produced by *P. javanicum* determined by Ward and Jamieson (1934) was found to contain oleic, linoleic, palmitic, stearic, and tetracosanic acids. The fat produced was reported to be entirely different from that earlier isolated by Browne (1906) from an unidentified *Citromyces*. May and Ward (1934) reported that the chitinous complex formed 17.4 per cent of the fat free tissue of the mold mycelium. The degradation and chemical composition of this fraction was investigated.

Fat production by *Penicillium javanicum* has been studied also by Garoglio and Ciferri (1940), who reported yield of fat up to 9 per cent based upon the sugar consumed, and by Soeters (1941), who reported 5 to 6 per cent yield. Yields obtained in both cases approximated those earlier reported by Lockwood and co-workers, which, when calculated upon the same bases, ranged from 6 to 8.15 per cent.

Taufel, *et al.* (1937) discussed fat production by *Citromyces* sp., a form which may or may not be closely related to *Penicillium javanicum*.

Penicillium ehrlichii Klebahn was reported by Ehrlich (1932), its dis-

coverer, to produce a pectolase which rapidly hydrolyzes pectolic acid into pectolactonic acid and further into molecular d-galacturonic acid. The enzyme was not found in yeasts, but was demonstrated in Taka-diastase, in some green *Penicillium* designated *P. glaucum*, and in the snail, *Helix*.

Oxford, Raistrick, and Simonart (1935) isolated fulvic acid, a crystalline yellow pigment from *Penicillium brefeldianum* Dodge. The same pigment was found in *P. griseo-fulvum* Dierckx (see p. 536) and *P. flexuosum* Dale (see p. 534).

No biochemical or physiological studies have yet been made on Raper and Fennell's new species *Penicillium parvum* and *P. levitum* (1948).

Hettinger (1934) published a doctoral dissertation on the morphology and physiology of *Penicillium zukalii* Biourge. In the same year, and using the same culture, Hornung published a dissertation on the physiology and biochemistry of this species. When received by us a few years later, the culture was found to represent a typical strain of *Penicillium brefeldianum*. The culture which they used had been received directly from Biourge.

Penicillium thomii Series

Outstanding Characters

Sclerotia characteristically produced, but in some species not developed upon all substrata (including Czapek's solution agar); typically hard and gritty, but in some species consisting of comparatively soft masses of pseudoparenchymatous cells.

Colonies typically rather fast growing, developing abundant sclerotia which often characterize the colony appearance, but in some species slow growing and developing sclerotia only on certain substrata.

Conidiophores abundant in some species, not in others; arising from the substratum, to produce a velvety effect, or from trailing vegetative hyphae; from very short up to 300 to 400μ long; walls smooth or delicately echinulate.

Penicilli monoverticillate, usually strictly so but sometimes showing an independent branch, sparsely produced in some species and strains; typically showing parallel sterigmata in compact clusters.

Conidia mostly elliptical to subglobose, smooth-walled, 2.5 to 3.5μ in diameter, borne in long chains often adherent in loose columns.

Series Key

a. Sclerotia produced upon all substrata, hard, brittle, crushing with difficulty, composed of thick-walled sclerenchyma-like cells.....*P. thomii* series

1′. Sclerotia uncolored or nearly so, borne in small clusters surrounded by conspicuous envelopes of bright orange-red mycelium

P. sclerotiorum van Beyma

2′. Sclerotia in flesh to pink shades, not in clusters and not embedded in masses of orange-red hyphae.....*P. thomii* Maire

3′. Sclerotia in orange-brown shades, not in clusters, often surrounded by a loose network of yellow to orange or light brown mycelium....*P. lapidosum* n. sp.

b. Sclerotia produced upon some substrata, not on others including Czapek, comparatively soft, composed of pseudoparenchymatous cells with walls thickened. *P. turbatum* sub-series

1′. Colonies on Czapek agar not developing dull dark purple colors in reverse, somewhat restricted.....*P. turbatum* Westling

2′. Colonies on Czapek agar developing dull, dark purple colors in reverse, very restricted.....*P. pusillum* Smith

Briefly characterized, the *Penicillium thomii* series comprises a group of monoverticillate Penicillia which regularly produce sclerotia. As a matter of convenience, the series may be subdivided as follows: (1) the series proper, wherein the member-species produce abundant sclerotia upon all substrata, and the sclerotia are very hard, brittle, and crush with difficulty; (2) the *P. turbatum* sub-series, in which sclerotia are not produced upon some substrata (including Czapek agar), and the sclerotia are softer and represent less compact masses of thick-walled cells.

In general appearance, form, and texture the sclerotia of *Penicillium thomii* and allied species are strikingly similar to those produced by *P. raistrickii* Smith, a consistently biverticillate species (see p. 275). The degree of relationship between the two series, of which these species are representative, has not been worked out, but there is a definite possibility that the two will tend to merge as more and more sclerotium-producing strains are examined. At the same time the sclerotia of *P. thomii*, etc. are strongly suggestive of the late-ripening perithecia of certain ascosporic species such as *P. parvum* Raper and Fennell (p. 138), in the *P. javanicum* series, and *P. asperum* (Shear) n. comb. (p. 263), in the *Carpenteles* series. In early stages of development the perithecia of these latter species are strikingly similar to the sclerotia of *P. thomii* in form and texture, and reveal apparent differences only after 3 to 4 weeks or more when asci begin to appear in limited central areas of the previously completely sclerotioid bodies. The process of ripening and attendant ascospore formation may proceed until only a thin outer wall 2 to 3 cells in thickness remains, or it may cease at any time prior to this, and under certain conditions, as yet not adequately explored, it may never be initiated. In the latter case the potential perithecium remains in effect a sclerotium. There are then a number of considerations which seem to tie these different ascosporic and/or sclerotial series together, and it may eventually become desirable to group together into a single section all of the species now regarded as comprising the monoverticillate *P. javanicum* (ascosporic) and *P. thomii* (sclerotial) series and the biverticillate *Carpenteles* (ascosporic) and *P. raistrickii* (sclerotial) series.

In the series proper, *Penicillium thomii* Maire is the oldest, best known, and most abundant species, apparently being world-wide in distribution. A form approximating this species was reported and described as culture No. 29, without a name, by Thom in 1910. Subsequent to this, Maire (1917), investigating the fungi of North Africa, described a sclerotial form as *P. thomii* and called attention to similarities between his species and Thom's culture. The species as now recognized represents a common soil type characterized by the production of pink sclerotia, often in sufficient numbers to characterize the colony. Penicilli are abundantly produced upon most media, are strictly monoverticillate, and bear elliptical to subglobose, smooth-walled conidia (fig. 43A).

Van Beyma in 1937 described *Penicillium sclerotiorum* in terms which clearly aligned it with *P. thomii*, a placement confirmed by examination of the type strain. It differs from *P. thomii* primarily in producing almost colorless sclerotia in limited clusters or 'nests' that are surrounded by loose envelopes of bright orange-red mycelium. Such islands of brilliantly colored mycelium may occur somewhat scattered throughout the colony, or they may be massed together to form a continuous layer in which conidial structures occur either scattered or in small localized areas. The penicillus (fig. 43B) is essentially like that of *P. thomii*. The species was originally isolated in Java, but has since been obtained from other sources, mostly of tropical or subtropical origin. It appears to be less widely distributed than *P. thomii*.

Penicillium lapidosum Raper and Fennell (1948) is based upon a culture isolated by Williams, Cameron, and Williams (1941) from canned blueberries. The species is unusually heat-resistant. It is characterized by its rapid growth, its abundant orange-brown sclerotia, and its sparse production of conidial structures (fig. 43C) upon most substrata. *Penicillium mangini* Duché and Heim (1931), a sclerotial species not recognized in this Manual for reasons cited elsewhere (see p. 165), is regarded as possibly approximating *P. lapidosum*.

Two species comprise the *Penicillium turbatum* sub-series, namely: *P. turbatum* Westling and *P. pusillum* Smith. Both are characterized by their failure to produce sclerotia upon Czapek agar and also their more restricted growth upon this substratum. In these species, sclerotia are softer and easily crushed. The degree of relationship between them and the members of the *P. thomii* series proper is open to some question. However, they possess certain characters in common and it is believed that they can be keyed here more satisfactorily than elsewhere.

Penicillium thomii Maire, in Bul. Soc. Hist. Nat. Afrique du Nord. **8**: 189–192. 1917. See also, Thom, U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, p. 78. 1910; also The Penicillia, p. 173. 1930.

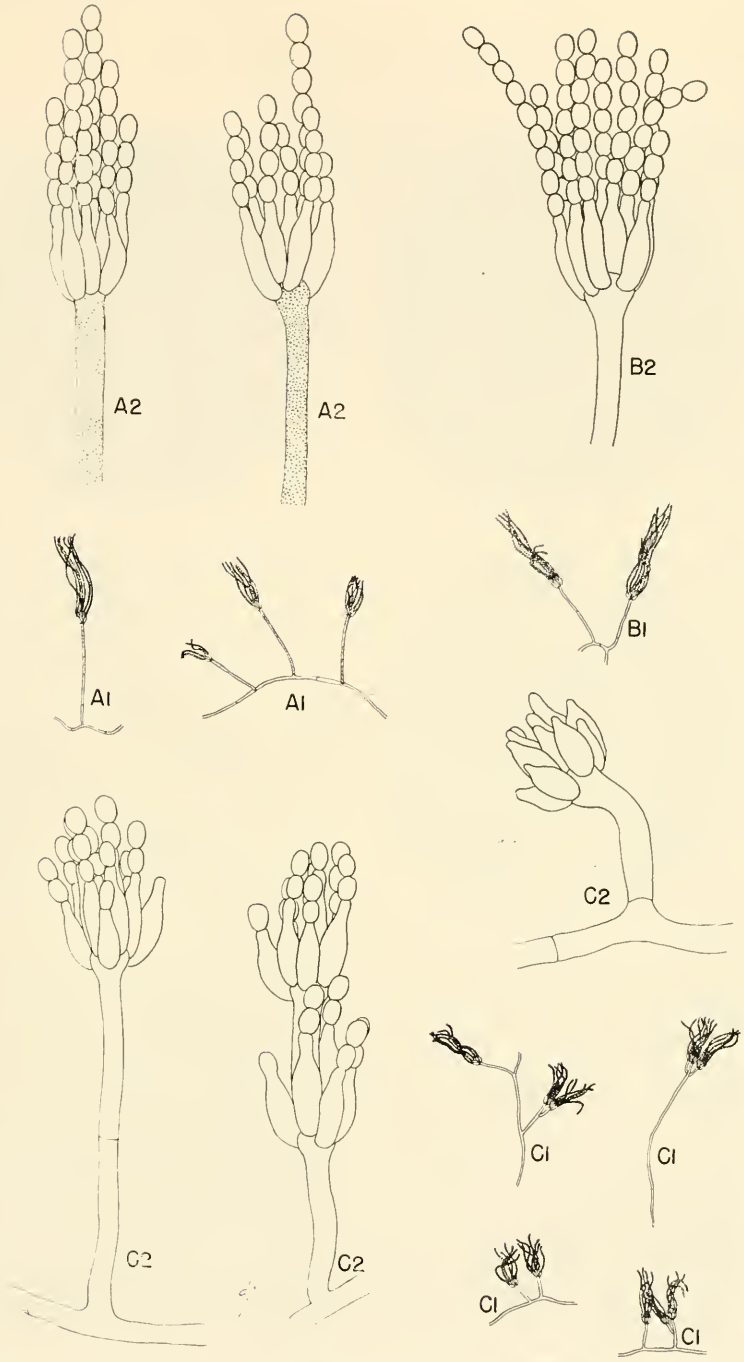


FIG. 43. The *Penicillium thomii* series. *A*, *P. thomii* Maire: A_1, Habit sketches of representative penicilli, × 140; A_2, Penicilli of the same species seen under oil immersion, × 1400—note the delicately echinulate character of conidiophore walls. *B*, *P. sclerotiorum* v. Beyma: B_1, Habit sketch of penicilli, × 140; B_2, Detail of single penicillus, × 1400. *C*, *P. lapidosum* Raper and Fennell: C_1, Habit sketches, × 140; C_2, The same under oil immersion showing cellular details and variations in structure, × 1400.

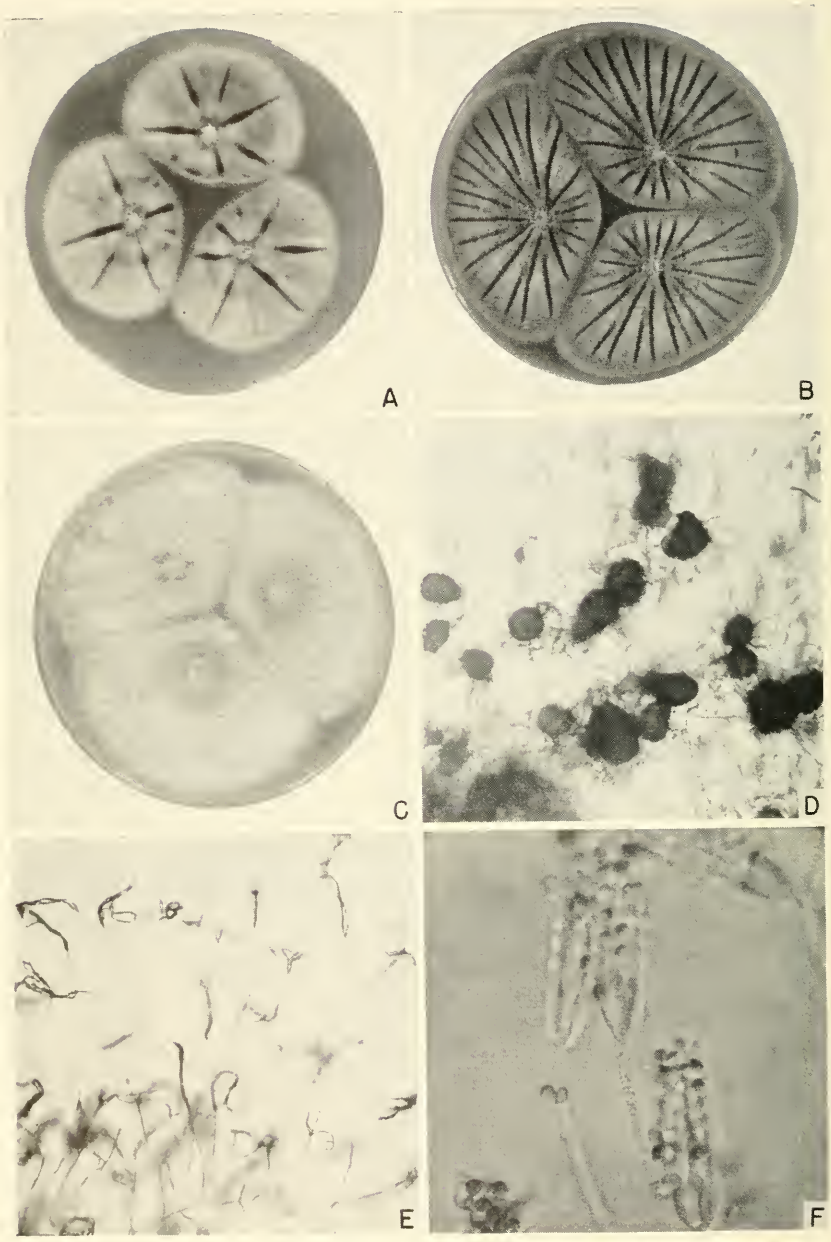


FIG. 44. *Penicillium thomii* Maire, NRRL 1640. *A*, *B*, and *C*, Two-week-old colonies on Czapek, steep, and malt agars, respectively. *D*, Sclerotia as developed on hay agar, × 65. *E*, Penicilli as seen in thin marginal area of colony on Czapek agar, × 65. *F*, Detail of penicilli, × 900.

Not *P. thomi* Zaleski, in Bul. Acad. Polanaise Sci.: Math. et Nat. Ser. B, 492–493, Taf. 56. 1927.

Colonies on Czapek's solution agar growing fairly rapidly in most strains, attaining a diameter of 3.5 to 4.0 cm. in 10 to 12 days at room temperature, occasionally more restricted, conspicuously furrowed (fig. 44A), consisting of a tough basal felt with surface appearing loose to slightly floccose, white to pale blue-green, sporulating lightly throughout but more abundantly in central colony areas and in localized sectors, in gray-green shades from court gray to pea green (Ridgway, Pl. XLVII), sometimes producing abundant, hard, rounded to oblong, pink sclerotia, up to 300 to 350μ in diameter throughout the colony area (fig. 44D), sometimes in limited sectors only, and often failing to develop sclerotia, especially in strains long maintained in artificial culture; exudate clear, abundantly produced in some strains, not in others; odor slight, suggesting mushrooms; reverse in pale yellow to pinkish brown shades; penicilli strictly monoverticillate, bearing conidial chains usually in loose columns up to 150μ or more in length; conidiophores arising from the basal felt and from interlacing aerial hyphae (fig. 44E), seldom branched, with walls delicately echinulate (fig. 43A), variable in length up to 300 to 400μ by 3.0 to 3.5μ, with apices enlarged, somewhat vesicular about 4.0 to 5.0μ in diameter; sterigmata mostly parallel, in crowded clusters, commonly 8 to 12 in the verticil, usually 8 to 10μ by 2.0 to 2.5μ, with conidium-bearing tips somewhat narrowed; conidia elliptical to subglobose, mostly 3.0 to 3.5μ in long axis, smooth-walled (figs. 43A and 44F).

Colonies on steep agar spreading broadly, 5 to 6 cm. in 10 to 12 days at room temperature, radially furrowed (fig. 44B), velvety in most strains but with surface appearing loosely floccose in some, usually heavily sporing throughout, in yellow-green shades near gnaphalium to pea green (R., Pl. XLVII), becoming dull gray shades in age; sclerotia as described above, abundantly produced in some strains, not in others, developing adjacent to the substratum, commonly obscured by overlying hyphae and conidial structures, in other cases dominating the colony; penicilli as described above.

Colonies on malt agar spreading, not furrowed, somewhat less heavily sporing, often showing more aerial mycelium (fig. 44C); commonly producing sclerotia more abundantly, in some strains forming a dense, continuous layer adjacent to the substratum and lending to the colony an orange-pink color interrupted only by areas of heavy conidial development; penicilli as described on Czapek but with conidiophores more conspicuously and closely echinulate.

Species description centered upon NRRL 702, received from Ross W. Davidson, Washington, D. C. in 1934, as an isolate from wood; NRRL 703,

received in 1936 from Professor Westerdijk as a culture of this species contributed by Stapp and Bortels (Berlin), as a soil isolate; NRRL 1640, contributed by D. H. Linder, Natick, Massachusetts, as an air contaminant; NRRL 2077, from Wm. H. Weston in June 1945, as an isolate from a pine cone; and numerous other strains examined during the course of our investigations over a period of many years.

The species is abundant and cosmopolitan in distribution. It is especially common in soil and has been repeatedly obtained from lumber and other wood products. When first isolated, strains almost invariably produce abundant pink sclerotia, but with continued laboratory cultivation tend to become increasingly conidial. Strains long maintained in collections often completely lose their ability to produce these characteristic structures. Members of the species are subject to considerable variation in culture, and the same colonies may contain sectors that are either predominantly conidial or sclerotial. In addition to variation in the relative abundance of sclerotia and conidial structures, occasional strains show sclerotia less definitely pink in color, and produce smaller conidial structures as short branches from interwoven aerial hyphae. This development is suggestive of the *Penicillium decumbens* series, although sclerotia have not been reported for any of the species that comprise that series.

Unlike *Penicillium sclerotiorum* where sclerotia are borne in clusters within envelopes of brightly colored sterile hyphae, the sclerotia of *P. thomii* are borne singly and are naked or nearly so. The conidial apparatus of the two species are strikingly similar.

In 1910 (p. 78), Thom published descriptive notes on a culture, No. 29, but did not assign to it a specific name. Maire published his description of *Penicillium thomii* in 1917 and noted slight differences between his culture and Thom's No. 29. The differences, however, were minor in character and there was little question that the two investigators were dealing with strain differences in two members of the same species. Accordingly, Thom, in 1930, regarded his No. 29 (then lost from his collection) as representative of Maire's species. Since that time the species concept has been further broadened and today we tend to regard as representative of *P. thomii* Maire all monoverticillate strains producing hard, brittle sclerotia that are pink in color.

Penicillium sclerotiorum van Beyma, in Zentbl. f. Bakt. etc., (II) **96:** 416–419, figs. 1 and 2. 1937.

Colonies on Czapek's solution agar growing somewhat restrictedly, attaining a diameter of 2.0 to 3.5 cm. in 10 to 12 days at room temperature, variable in color and texture depending upon the relative abundance of sclerotia, vegetative hyphae, and conidial structures; varying from essen-

tially conidial presenting a velvety appearance, through more or less floccose from the development of abundant vegetative mycelium, to predominantly sclerotial with limited development of fruiting structures or of aerial

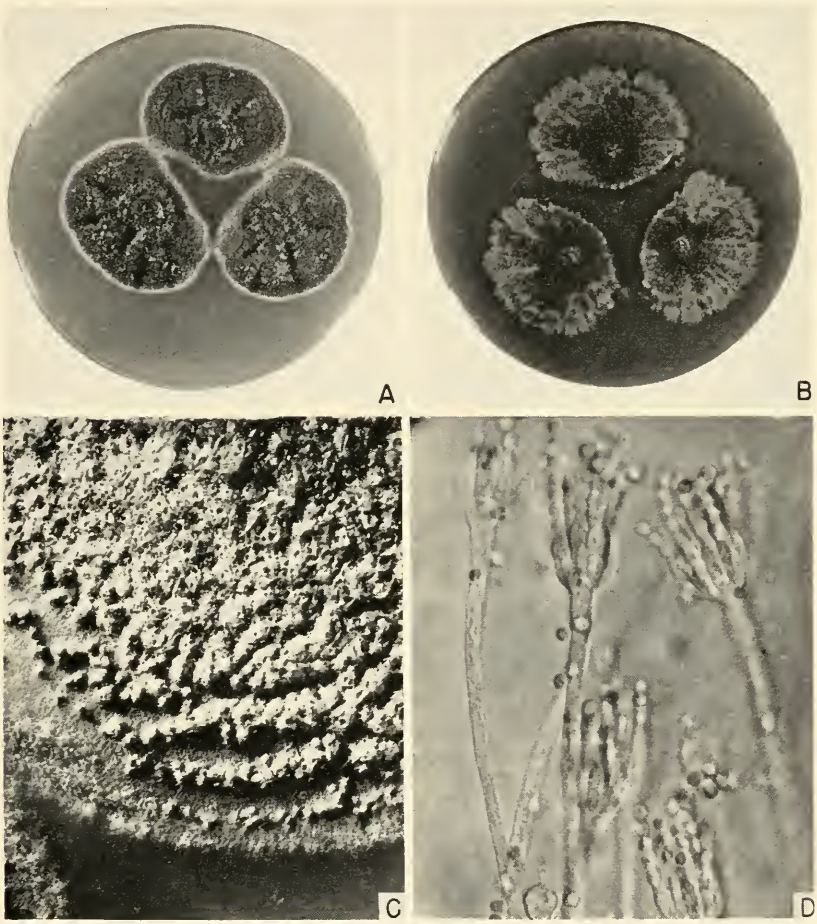


FIG. 45. *Penicillium sclerotiorum* v. Beyma, NRRL 2074. *A* and *B*, Two-week-old colonies on Czapek and malt agars; the former is characterized by a heavy and consistent development of sclerotia, the latter by alternating conidial areas (light) and massed sclerotia (dark). *C*, Colony margin showing massed clusters, or "nests," of sclerotia, × 5. *D*, Detail of penicilli, × 900.

vegetative hyphae (fig. 45A), frequently showing these different aspects as sectors in the same colony; conidial structures limited or abundant, at first arising primarily from the substratum and *en masse* producing areas near artemisia green (Ridgway, Pl. XLVII), in age often developing from aerial

hyphae over the entire colony surface; vegetative mycelium in orange-red shades; sclerotia uncolored or nearly so, typically borne in fairy definite clusters surrounded by envelopes of sterile encrusted hyphae (fig. 45C) in bright orange-red shades near scarlet to Brazil red (R., Pl. I), usually occurring in limited sectors but sometimes characterizing the entire colony when young; exudate colorless or nearly so, abundantly produced in areas of heavy sclerotial or mycelial development, lacking or limited in amount in predominantly conidial areas; odor slight, suggesting mushrooms; reverse in yellow to orange-red shades, not diffusing into the surrounding agar; penicilli strictly monoverticillate, bearing conidia in parallel chains forming loose columns up to 150 to 200μ in length by 15 to 20μ wide; conidiophores arising from the substratum or from aerial hyphae, seldom branched, smooth-walled, up to 200 to 300μ in length by 3.0 to 3.5μ, enlarging in terminal areas to vesicular apices 5.0 to 7.0μ in diameter; sterigmata parallel, in crowded clusters of 12 or more, mostly 8 to 10μ by about 2.0μ, with conidium-bearing tips somewhat narrowed; conidia elliptical, about 2.5 to 3.0μ by 2.0 to 2.5μ, smooth-walled (figs. 43B and 45D).

Colonies on steep agar (Col. Pl. III) growing more rapidly, 4.0 to 5.0 cm. in 10 to 12 days at room temperature, in texture and appearance essentially as on Czapek but with predominantly conidial and sclerotial sectors more pronounced; penicilli as described above.

Colonies on malt agar spreading, up to 5.5 cm. in 10 to 12 days at room temperature, thin, usually heavy sporing, with conidial areas velvety and light blue-green; sclerotia abundantly produced, in limited clusters projecting through the conidial layers and appearing as bright red islands (fig. 45B); penicilli as described above but with conidiophore walls delicately roughened.

Species description based upon van Beyma's type, isolated originally by Professor Boedijn from air (?) in Buitenzorg (Java). This culture was received by us in October 1945, from the Centraalbureau and has since been maintained in our collection as NRRL 2074. The species is represented also by NRRL 2076, isolated in 1946 from a sample of soil from South Africa; and has been seen occasionally among cultures originating from deteriorating military equipment that have been examined by us but not maintained in the collection.

Penicillium sclerotiorum is characterized particularly by its prominent sclerotia. As noted by van Beyma (1937), these are essentially colorless, often somewhat angular in pattern, and range up to 200 to 400μ in diameter. They are very hard, "stone-like" and are composed of thick-walled sclerenchyma-like cells 10 to 15μ in diameter. In most cultures they occur in small clusters, closely compacted together and are contained within an envelope of sterile hyphae whose walls are studded with a bright orange-red

pigmented substance appearing almost crystalline. As reported by van Beyma the pigment is readily soluble in alcohol, ether, and other solvents, but insoluble in water. Van Beyma recorded sclerotia as somewhat larger (500 to 700μ) than observed in our cultures and reported that they were produced more abundantly at temperatures of 25 to 26°C. than at temperatures below 20°C.

The species differs from *Penicillium thomii* Maire primarily in the production of abundant bright red mycelia accompanying the sclerotia, and in producing conidiophores with walls smooth or nearly so on Czapek's solution agar, although delicately roughened on malt agar. It is closely related to *P. thomii*.

Penicillium lapidosum Raper and Fennell, in Mycologia **40**: 524–527, fig. 6. 1948; also Williams, Cameron, and Williams in Food Research **6**: 69–73. 1940.

Colonies on Czapek's solution agar spreading broadly, attaining a diameter of 5.0 to 6.0 cm. within 2 weeks at room temperature, plane or lightly furrowed (fig. 46A), golden orange in color, developing reddish tints in age, consisting of an extensive vegetative mycelium largely submerged, developing abundant orange-brown sclerotia in a fairly dense layer on the agar surface, with limited development of sterile aerial hyphae often more or less obscuring the individual sclerotia; penicilli rarely produced and not affecting the colony appearance (see description on hay agar below); exudate abundant, in orange-red shades; odor lacking or indistinct; reverse in orange-red shades becoming deep reddish brown in age; sclerotia globose to subglobose, variable in size up to 300 to 350μ in diameter (fig. 46C), very hard, crushing with difficulty, composed of very thick-walled polygonal cells mostly 10 to 15μ in diameter.

Colonies on steep agar as on Czapek but growing even more rapidly and generally producing more abundant exudate and more intense coloration in reverse; penicilli very sparsely produced; sclerotia as above.

Colonies on malt agar spreading broadly, plane (fig. 46B), quickly developing golden yellow shades from abundant orange colored sclerotia and enveloping yellow encrusted sterile hyphae; exudate abundant, clear; penicilli developing fairly abundantly in older colony areas but not affecting the overall appearance of the culture.

Colonies on hay infusion agar growing rapidly, thin, consisting of a spreading, submerged vegetative mycelium, producing sclerotia in limited numbers in a thin layer on the agar surface with these surrounded by and overgrown with a thin network of interwoven and trailing vegetative hyphae bearing numerous penicilli on short lateral branches or conidiophores; sclerotia as described above but generally smaller, rarely exceeding 200μ in

diameter; penicilli variable, mostly strictly monoverticillate, consisting of compact verticils of sterigmata bearing tangled or loosely parallel chains of conidia up to 100μ in length, occasional penicilli once or twice branched and producing two or more clusters of sterigmata (fig. 43C), conidiophores mostly 25 to 75μ, rarely more than 100μ in length by 2.5 to 3.0 or 3.5μ in

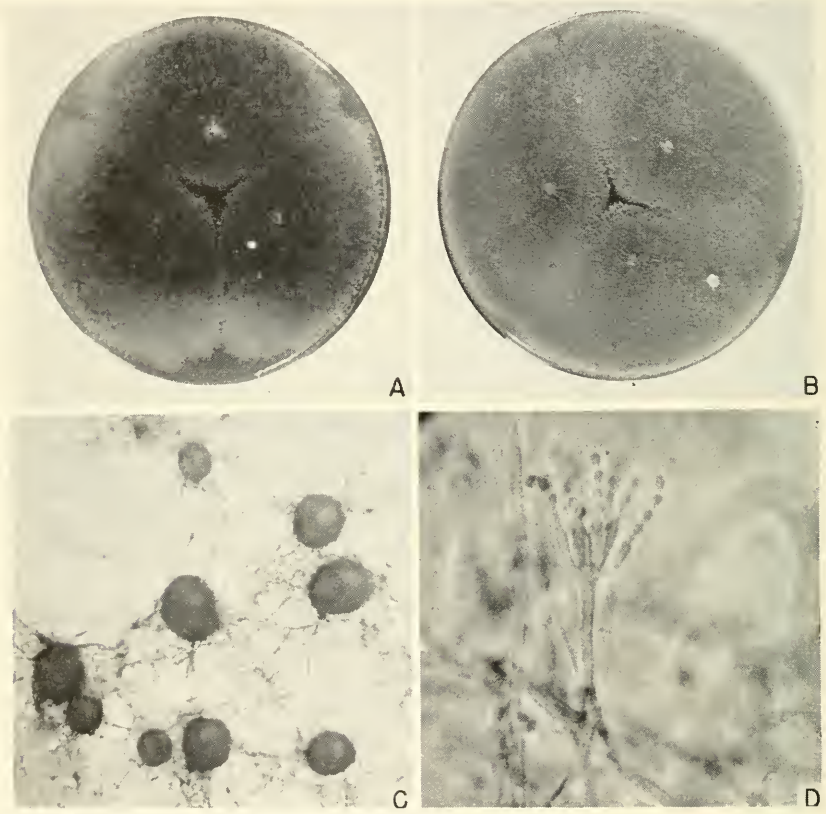


FIG. 46. *Penicillium lapidosum* Raper and Fennell, NRRL 718. *A* and *B*, Two-week-old colonies on Czapek and malt agars. *C*, Sclerotia as seen in corn meal agar, × 65. *D*, Detail of penicillus, × 900.

diameter, with walls smooth, commonly septate; branches, when present, mostly 10 to 20μ by 2.5 to 3.0μ, more or less divergent; sterigmata ranging from 3 or 4 up to 7 or 8 in the verticil, mostly 6.0 to 7.5μ by about 2.0μ with conidium-bearing tips definitely narrowed; conidia at first definitely elliptical, usually remaining so and ranging from 2.5 to 3.0μ by 2.0 to 2.5μ, occasionally subglobose 2.0 to 2.5μ in diameter, with walls smooth and comparatively heavy (figs. 43C and 46D).

Species description based upon NRRL 718 isolated in 1938, from canned blueberries, by Dr. E. J. Cameron and associates, National Canners Association, Washington, D. C. This was one of two Penicillia isolated by these investigators and submitted to Thom for identification. They were subsequently incorporated into the NRRL Collection without name, but were early recognized as different: One produces large striate ascospores and is cited by Raper and Fennell (1948) as the type for their new species *Penicillium striatum* (see p. 606); the second produces abundant, large sclerotia and constitutes the type of the species under consideration (see also Raper and Fennell, 1948). In their paper published in 1940, Williams, Cameron, and Williams reported the sclerotia of the latter mold to be unusually heat-tolerant, being able to withstand a temperature of 90.5°C. for 30 to 40 minutes. The culture also was reported to be able to grow (or survive) in a high vacuum. Williams, *et al.* reported the successful isolation of the mold from three of five soil samples collected from blueberry fields and heated in the laboratory to 180°F. for 25 minutes. They failed, however, to distinguish between the form which produced ascospores and that which produced sclerotia—in fact, they apparently regarded the two strains as representing different aspects of the same fungus which they reported as an undescribed species of *Penicillium*. Their report failed to say whether both types, sclerotial and ascosporic, were reisolated from soil or whether the sclerotial form only was so obtained.

The type strain of *Penicillium lapidosum* is characterized particularly by the abundant sclerotia which it produces. In appearance and texture, these are strongly suggestive of the young, sclerotioid perithecia which characterize certain ascosporic Penicillia such as *P. parvum*, *P. baarnense*, and *P. asperum*. At no time, however, have we observed any evidence of ascospore formation in this strain—the bodies remaining hard and sclerotioid indefinitely.

A second culture, essentially duplicating NRRL 718, isolated at Baarn in 1939, was received in June 1946, from the Centraalbureau as *Penicillium mangini* Duché and Heim. This is now maintained in our Collection as NRRL 2084. The above cultures seem to agree reasonably well with Duché and Heim's description both in the character of the sclerotia produced and in the manner in which the penicilli are borne on trailing aerial hyphae. Furthermore, the penicilli are not consistently monoverticillate but frequently produce branched structures of the type illustrated by Duché and Heim (1931). Were it not for the fact that Duché, in personal conference with us in our Laboratory and with the cultures in question before him (January 1947), indicated that his species was originally based upon a different type of organism, we would have concluded that NRRL 718 and 2084 accurately represented *P. mangini*. However, since these forms ap-

parently do not represent his species, and since they could not be satisfactorily assigned to any other described form, Raper and Fennell (1948) recognized them as representative of a new species to which they assigned the binomial *P. lapidosum* because of the abundant stone-like sclerotia that characterize it.

Penicillium turbatum Westling, in Arkiv för Botanik **11**: 54, 128–130; figs. 36, 74a and b. 1911. Also Thom, The Penicillia, p. 207. 1930.

Colonies on Czapek's solution agar growing somewhat restrictedly, attaining a diameter of 2.5 to 3.0 cm. in 2 weeks at room temperature, strongly buckled and wrinkled, comparatively close-textured, thin, velvety, zonate, central areas white to light gray with limited sporulation, marginal area 0.5 to 1.0 cm. wide fairly heavy sporing, in dull gray-green shades near storm gray or olive gray (Ridgway, Pl. LII); odor indistinct, indefinite; exudate lacking or limited in amount; reverse in cream to light yellow shades with some traces of green; conidiophores usually arising directly from the substratum, less commonly from creeping hyphae, short, mostly 40 to 70μ but ranging from 10 to 100μ in length by 2.5 to 3.5μ in diameter, with walls smooth, usually bearing strictly monoverticillate penicilli but occasionally showing one independent branch; conidial chains 50 to 100μ long, tangled; sterigmata few in the verticil, commonly 4 to 8, mostly 10 to 14μ by 2.2 to 3.0μ, having fairly long tapered conidial tubes; conidia elliptical, smooth, 3.5 to 5.5μ in long axis by 2.5 to 4.0μ in diameter, mostly 4.0 to 4.5μ by 3.0 to 3.5μ.

Colonies on steep agar as on Czapek in rate of growth and general colony pattern but consistently heavier sporing and usually producing abundant conidial structures over the entire colony surface, at first bluish gray but quickly assuming dull olive gray shades; definitely zonate, ridged; reverse as on Czapek but in dull shades; producing abundant sclerotia adjacent to the agar surface but these partially obscured by overlying conidial structures, up to 150μ in diameter, colorless to yellowish, composed of polyhedral cells up to 10 to 15μ in diameter with walls 1 to 2μ thick; conidial structures as on Czapek.

Colonies on malt extract agar spreading rather broadly, 4.0 to 5.0 cm. in 10 to 12 days, thin, plane except slightly raised in center, velvety, in pale gray shades; producing scattered sclerotia as described on steep agar (fig. 47); penicilli as described on Czapek.

Species description centered upon NRRL 757, received in 1911 from Westling as type and subsequently maintained in the Thom collection as number 2545. A second culture, duplicating NRRL 757, was received from Biourge in 1924 as *Penicillium turbatum* Westling. This was included in Thom's collection as number 4733.122 (now maintained as NRRL 758)

and was discussed under this number by him in connection with this species in his Monograph (1930).

When grown on malt extract and steep agars, the species is characterized by the production of definite sclerotia, or sclerotia-like bodies. Such structures have not been observed in our cultures grown on Czapek agar, nor were they apparently observed by Thom in 1930. Biourge likewise failed to report such structures although the strain obtained from his laboratory shows them in equal abundance to the strain obtained from Westling directly. In his original description based upon colonies grown on prune gelatine, Westling (1911) reported the presence of numerous colorless to yellowish perithecia 55 to 105μ in diameter, which Thom (1930, p. 207)

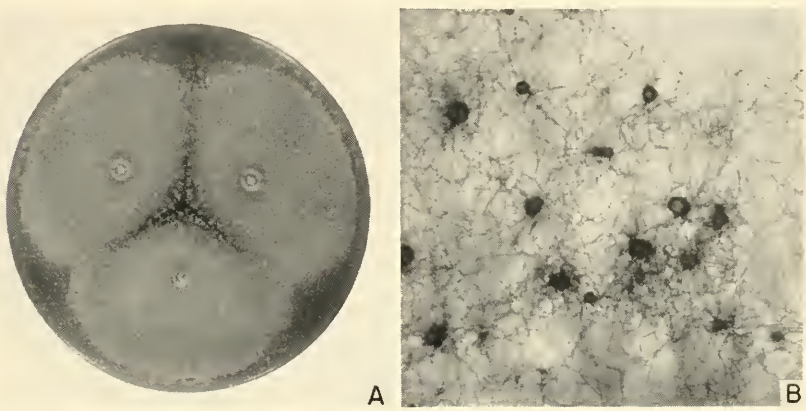


FIG. 47. *Penicillium turbatum* Westling, NRRL 757. *A*, Two-week-old colony on malt agar. *B*, Sclerotia as seen in marginal colony area, × 65.

interpreted as sclerotia since no ascogenous stage was reported. Repeated examination of these structures in our current study has likewise failed to show any sign of asci or ascospores.

The presence of sclerotia in a strictly monoverticillate form having elliptical conidia suggests close relationship to *Penicillium thomii* Maire. The sclerotia in *P. turbatum*, however, differ markedly from those of *P. thomii*. They are consistently smaller, comparatively soft, crush easily, and are composed of parenchyma-like cells with walls only moderately thickened. The species is keyed adjacent to the *P. thomii* series but is regarded as somewhat separate from it because of the difference in sclerotia.

Penicillium pusillum Smith, in Brit. Mycol. Soc. Trans. **22:** 254–255, Pl. XVI, figs. 7 and 8. 1939.

Author's diagnosis as follows:

"Colonies on Czapek agar growing very slowly and restrictedly, attaining a diameter of about 1 cm. in 12 days and thereafter spreading very little, pale bluish gray, gradually becoming overgrown with white to vinaceous mycelium, thin and tough,

with surface growth consisting of trailing hyphae and ropes of hyphae, usually with centre depressed or folded and wrinkled; reverse dark dull purple becoming very deep brownish purple, with colour diffusing slightly into medium; drops colourless; dense masses of compacted mycelium formed but no true sclerotia; colonies on wort agar growing somewhat more rapidly than on Czapek agar, at first white, with patches of greyish green, slightly floccose and funiculose, wrinkled and buckled, after a few days developing masses of pale buff to pinkish brown sclerotia; reverse brownish; conidiophores arising from trailing hyphae and ropes of hyphae, mostly simple but with an occasional branch, 35 to 55μ by 1.5 to 2.0μ, smooth, slightly swollen at apex; penicilli mostly strictly monoverticillate but occasionally, especially on Czapek agar, with one or two sterigmata proliferating and developing single crosssepta (i.e. with occasional metulae mixed with sterigmata); sterigmata almost cylindrical, 10 to 11 (15)μ by 1.8 to 2.0μ; conidia smooth, ovate at first, becoming globose to sub-globose, 2 to 2.5μ diameter, or 2.3 to 2.8μ by 2.0 to 2.2μ; sclerotia brownish, irregularly globose, averaging 300μ in diameter, mostly confluent, composed of masses of irregularly globose or polygonal cells."

Isolated by Dr. G. E. Turfitt, Department of Biochemistry, London School of Hygiene and Tropical Medicine, University of London, from samples of dried blue peas. Maintained in the L.S.H.T.M. Collection as Catalogue No. 147 and so reported by Smith in his species diagnosis.

In discussing Turfitt's culture, Smith called attention to its very restricted growth on Czapek agar and to the curious dark dull purple reverse of colonies on this substratum. Growth on wort agar was more rapid and masses of sclerotia appeared after a few days. He compared the mold with other monoverticillate Penicillia known to produce sclerotia and concluded that it represented a new species, an opinion in which we concur.

As a monoverticillate *Penicillium* producing sclerotia, *Penicillium pusillum* is properly assignable within or adjacent to the *P. thomii* series. The species is suggestive of *P. phoeniceum* v. Beyma in the pigments developed in the colony reverse upon Czapek agar and also in the restricted character of its growth. In producing sclerotia upon wort agar but not upon Czapek, the species is strongly suggestive of *P. turbatum* Westling, wherein the same condition prevails. The latter species, as originally described, and as observed in our cultures, however, fails to develop any purple pigmentation. Believing the production of sclerotia by a mold to be more fundamental than the elaboration of similar colors, we are led to assign *P. pusillum* with *P. turbatum* rather than *P. phoeniceum*. The two species are regarded as constituting a sub-series characterized by the production of sclerotia upon some substrata but not on others, in contrast to the *P. thomii* series, in a strict sense, whose member-species regularly produce sclerotia upon all substrata.

Occurrence and Significance

Penicillium thomii Maire is widely distributed in nature. It is encountered in almost all soils examined, and commonly occurs on lumber and

other wood products stored in constant or intermittently moist environments. There is little evidence that the species is particularly significant, but its ubiquity undoubtedly indicates some role in general processes of decomposition. Examining the flora of forest soils and litter, Stapp and Bortels (1935) found *P. thomii* to be abundant and to be especially active in the decomposition of tannin. Kreutzfeldt-Plathe (1939a) found it to seriously impair the quality of stored butter and in this connection conducted a study of its metabolism under controlled conditions. Moore (1941) reported it as causing a leaf blotch of a cultivated *Cypripedium*. Karow, *et al.* (1944) reported the production of penicillic acid by *P. thomii*.

Penicillium sclerotiorum van Beyma is of special interest because of the brilliant orange-red color of the mycelia that characteristically surround the sclerotia of this species. The responsible pigment, designated sclerotiorine after the species name, was isolated by Curtin and Reilly (1940a and 1940b) and has been intensively studied by these and other workers at the University of Dublin. Sclerotiorine is a chlorine-containing compound ($C_{20}H_{20}O_5Cl$) insoluble in water but soluble in most organic solvents, which possesses the properties of an indicator, being wine red in NH_4OH solution and becoming golden yellow upon acidification with the end point somewhat clouded. Pigment in yields of 2 per cent can be obtained by extraction of the dried mycelium with petroleum ether, and crystallizes as fine hair-like yellow needles. Reilly and Curtin (1943) demonstrated that sclerotiorine production was not enhanced by increasing the amount of KCl in the medium, nor did replacement of this salt with KBr or KI yield other halide derivatives analogous with sclerotiorine. Pigment production is reduced as the $NaNO_3$ is increased from 0.2 to 0.4 percent, the metabolism of KCl being an inverse function of the nitrate concentration (Reilly, Long, and Curtin, 1944).

In addition to sclerotiorine, *Penicillium sclerotiorum* was found to produce a polysaccharide, termed sclerotiose, which upon isolation was found to represent a polyglucose (Albericci, Curtin, and Reilly, 1943). Maximum yields were obtained in neutral media with acid substrates having a hydrolysing effect. Sclerotiose production is favored by a low nitrate content, 10 percent yield being obtained in media containing 0.1 percent $NaNO_3$ against 3 percent yields in media containing 0.2 percent $NaNO_3$.

Penicillium turbatum Westling was reported by Florey, *et al.* (1944) to produce a penicillin-like antibiotic. Quantitative data were not supplied.

No biochemical or physiological studies of *Penicillium pusillum* Smith are known to us; or of *P. lapidosum* Raper and Fennell, aside from the studies of Williams, *et al.* (1940) on the heat resistance of its sclerotia.

Penicillium frequentans Series

Outstanding Characters

Colonies mostly fast-growing, usually spreading broadly, appearing velvety or with surface lightly floccose.

Conidiophores erect or ascending, rarely branched, with walls smooth to definitely roughened, arising from a basal felt or from trailing, looping, loosely interwoven aerial hyphae.

Penicilli strictly monoverticillate, comparatively large, with sterigmata forming a compact cluster, and with conidial chains usually in loose to compact columns.

Conidia globose to subglobose, rarely elliptical, from 2.5 to 5.0μ or more in diameter, and ranging from smooth to coarsely roughened, depending upon the species.

Series Key

1. Colonies velvety or nearly so, with conidiophores arising mostly from the substratum.
   a. Colonies generally spreading broadly on most media.
      1′. Conidia globose to subglobose.....*P. frequentans* series
         aa. Colonies with conidial areas strictly velvety and with reverse usually in orange-brown to reddish purple shades.
            1″. Conidia mostly 2.5 to 3.5μ, with walls thin, smooth or finely roughened.....*P. frequentans* Westling
            2″. Conidia mostly 4.0 to 5.0μ, with walls heavy, dark green, and coarsely roughened.....*P. purpurrescens* (Sopp) n. comb.
         bb. Colonies with conidial areas strictly velvety and with reverse usually in bright orange-red to red shades.....*P. multicolor* G.-M. and P. (see *P. implicatum* series, p. 196)
         cc. Colonies with surface loose-textured, with conidial structures arising from the substratum and from aerial mycelia, and with reverse uncolored, pinkish, or in purplish drab shades....*P. spinulosum* Thom

Members of this series are among the most widely distributed and the most abundant of all the Penicillia and many species assignable here have been described by different authors. Specific diagnoses have been based upon particular cultural or structural characteristics believed to be unique, less commonly upon the substrata from which the molds were first isolated. As would be expected in a series so abundant, marked variation between strains is regularly encountered. Viewing the series as a whole we believe it can best be separated into three reasonably well defined species aggregates centering around *Penicillium frequentans* Westling, *P. purpurrescens* (Sopp) n. comb., and *P. spinulosum* Thom (fig. 48). Each species aggregate is characterized by considerable variation within itself, and strains are not infrequently encountered which tend to bridge the lines of separation

we employ. Attempts at further separation would necessitate recognition of species based, in many cases, upon individual strain differences.

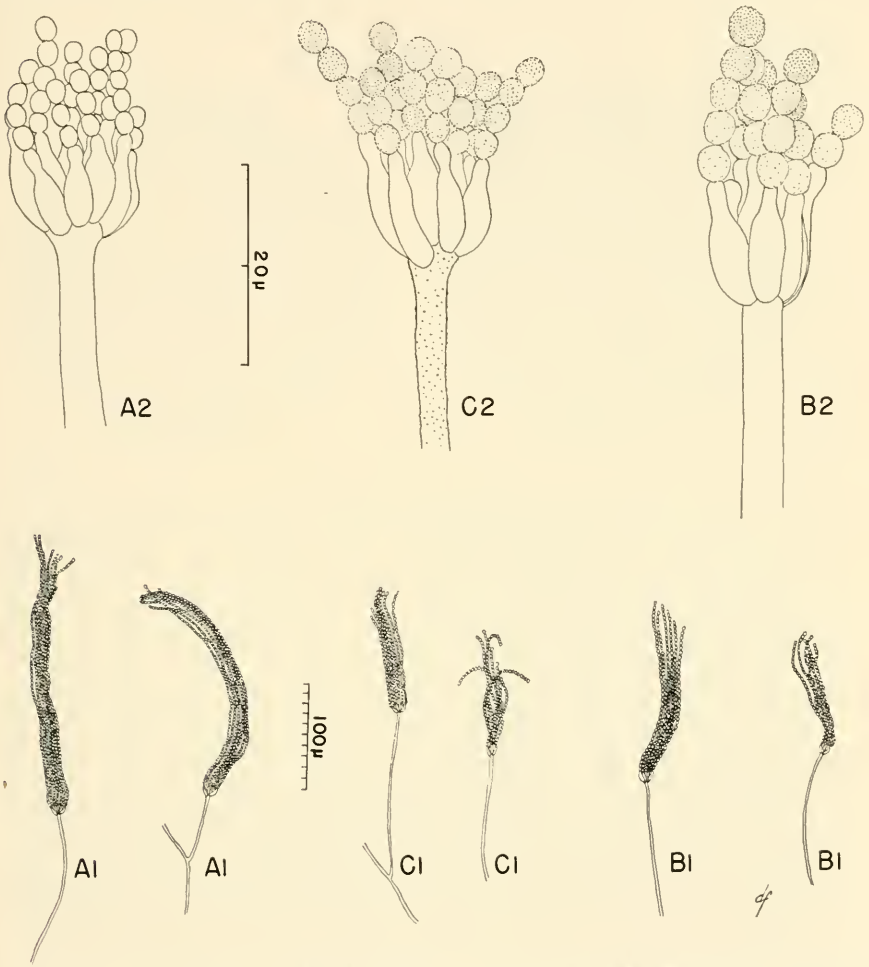


FIG. 48. *Penicillium frequentans* series. *A*, *P. frequentans* Westling: A_1, Habit sketches of penicilli showing characteristic columns of conidia; A_2, Typical penicillus seen under oil immersion. *B*, *P. purpurrescens* (Sopp) n. comb.: B_1, Habit sketch of conidial structures; B_2, Typical penicillus greatly enlarged. *C*, *P. spinulosum* Thom: C_1 and C_2, Habit sketches and detailed drawing of penicilli, respectively.

The separations proposed here may seem somewhat arbitrary to some workers, while to others it may appear that we have grouped together too large numbers of described and previously recognized forms. Suffice it to say, our treatment of the series is based upon careful comparative examina-

tion in culture of more than 50 strains, including the types of several species described originally by Biourge (1923), Zaleski (1927), Stapp and Bortels (1935), and others. The establishment of new species by these and other workers in many cases apparently resulted from the unavailability of type material of earlier authors and from the inadequacy of published descriptions. It is not surprising, therefore, that much duplication occurred. While some investigators may wish to recognize additional species in this general series, it is our belief that most workers will benefit by emphasizing broad relationships and trends rather than by the recognition of multiple species based upon minor and often variable strain characteristics.

Historically, the series is of considerable interest since it, in all probability, includes forms similar to those upon which Wehmer based his genus *Citromyces* and the two species, *C. glaber* and *C. pfefferianus* that he employed for the production of citric acid (1893b). No one can now say with certainty just what type of molds Wehmer used as the bases for his two species, although we believe *C. glaber* must have represented some form approximating *P. frequentans* Westling (see p. 176) and *C. pfefferianus* probably represented some form such as *P. spinulosum* Thom (see p. 184). Many additional investigators since Wehmer's time have attempted to utilize species of monoverticillate Penicillia (or *Citromyces* of Wehmer) for the production of citric acid but without notable success. Insofar as we know, selected strains of black Aspergilli, belonging to the *A. niger* group, are now regularly employed for the commercial production of this acid by fermentation methods.

Members of this series, especially *Penicillium frequentans* Westling and *P. spinulosum* Thom, are unusually common in soil and upon organic materials undergoing slow decomposition. No other species of the Monoverticillata, and few outside this group, are encountered more frequently. How important these organisms are in the decomposition of vegetable residue in nature has not been widely studied, but their common occurrence there is believed to indicate an active role in such processes.

Penicillium frequentans Westling, in Arkiv för Botanik **11:** 58, 133–134, figs. 39, 78. 1911. See also Biourge, Monograph, La Cellule **33:** fasc. 1, pp. 292–293, Col. Pl. X and Pl. XVII, fig. 99. 1923; and Thom, The Penicillia, pp. 216–217. 1930.

Colonies on Czapek's solution agar (Col. Pl. III) spreading rapidly, attaining a diameter of 5.0 to 6.0 cm. in 12 to 14 days at room temperature, broadly zonate, radiately wrinkled in most strains with central area commonly sulcate, thinning at the margin (fig. 49A), consisting of a closely woven felt of coarse hyphae either above or below the surface from which abundant crowded conidiophores arise, velvety, but commonly showing

limited trailing hyphae, heavily sporing, usually celandine to artemisia green (Ridgway, Pl. XLVII) becoming storm gray (R., Pl. LII) in age, in some strains darker, approximating American to dark American green (R., Pl. XLI); exudate limited, clear to light amber; odor faint, moldy; re-

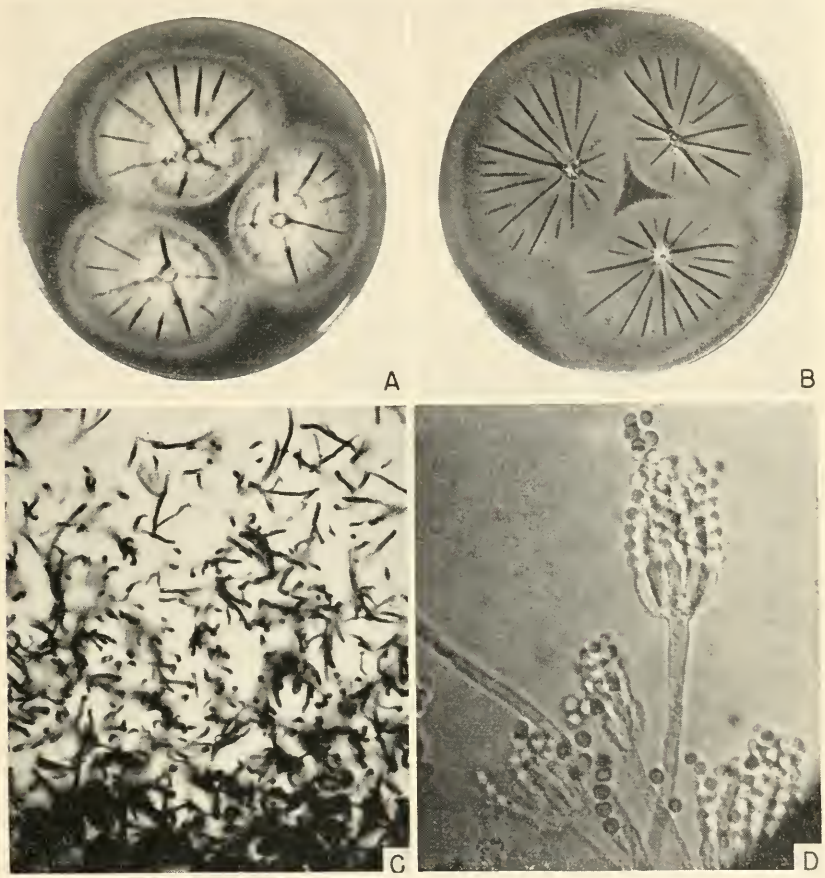


FIG. 49. *Penicillium frequentans* Westling, NRRL 1915. *A* and *B*, Two-week-old colonies on Czapek and steep agars. *C*, Low-power view of colony margin showing columnar character of conidial masses, × 40. *D*, Detail of penicilli, × 900.

verse mostly in shades of yellow-orange near russet to mars brown (R., Pl. XV), but in occasional strains appearing light purplish brown; conidiophores short, up to 100 to 200μ in length by 3.0 to 3.5μ in diameter, with walls smooth or finely roughened, and apices enlarged up to 5.0μ or more in width; conidial structures forming a crowded, fairly continuous layer over the whole culture (fig. 49C), with penicilli almost entirely monoverti-

cillate but showing an occasional branch; sterigmata in crowded clusters numbering 10 to 12 or more in the verticil, mostly 8 to 12μ by 3.0 to 3.5μ (fig. 49D), commonly producing chains of conidia in fairly well-defined columns up to 150μ or more in length, sometimes splitting in age, in other strains showing conidial chains only loosely parallel; conidia globose to subglobose, comparatively thin-walled, smooth or finely roughened, mostly 3.0 to 3.5μ in diameter.

Colonies on steep agar slightly larger than on Czapek, zonation reduced or lacking, velvety, radiately wrinkled, with texture as described above, heavily sporing (fig. 49B), quickly developing blue-green shades (see above), color in reverse deeper and somewhat more intense than on Czapek, with purplish tints more pronounced; penicilli as described above but with conidial chains in columns up to 200 to 300μ long.

Colonies on malt extract agar still larger, deeper and darker blue-green in color, almost plane, with traces of zonation at margin; reverse in dull dark brown shades; penicilli as on Czapek and steep agars but with conidial columns commonly up to 400 to 500μ in length, massed in a close stand and often breaking away when the culture dish is tapped.

Species description centered upon strains NRRL 1915 from George Smith, London School of Hygiene and Tropical Medicine, as No. Ad 6, labeled *Penicillium frequentans;* NRRL 1917 and 1918, from the same source as *P. frequentans*, designated No. Ad 67 and No. Ad 69 respectively; NRRL 763 from Z. I. Kertesz as a pectinase producer; and many additional strains similar in cultural appearance and in details of morphology. This species occurs in soil and upon decaying vegetable matter, and represents one of the most abundant and widely distributed of all the Penicillia. Westling's name is exceedingly appropriate.

In *Penicillium frequentans*, as in other widely distributed species of *Penicillium*, individual strains show appreciable variation in gross colony appearance and in the finer details of morphology. Gradations, however, are regularly encountered with the result that such variants do not stand apart as forms clearly separable, but rather seem to represent different aspects of an abundant and variable species. For example, strains are commonly isolated which show little or no roughness either of conidia or conidiophores and probably represent the basis of *P. glabrum* (Wehmer) Westling (see p. 176). Other isolates consistently show a limited roughness of conidia and commonly of conidiophores as well, and one of this type may have served as a basis for *P. flavi-dorsum* Biourge in which stalk and sterigmata walls were reported as squamulose (see p. 176). Limited variations in color also occur, with individual strains showing the range indicated in the description above. Almost invariably, strains of deeper green color produce conidia with walls definitely roughened.

In addition to such interspecies variation, other strains have been studied which merge *Penicillium frequentans* Westling almost imperceptibly into *P. spinulosum* Thom and *P. purpurrescens* (Sopp) n. comb. The latter species is distinguished chiefly by its large, heavy-walled, and coarsely roughened conidia, and by the production in most strains of a definite reddish purple pigmentation in the colony reverse. *Penicillium spinulosum*, on the other hand, is typically characterized by colonies of looser texture, with trailing hyphae usually abundant, and conidiophores less consistently erect and often arising from the aerial growth; conidia are spinulose and more definitely roughened than in *P. frequentans* but are not coarsely roughened as in *P. purpurrescens*.

The following species, described by other authors, are believed to be inseparable from Westling's *Penicillium frequentans*.

Citromyces albicans Sopp (Monograph, pp. 128–129, Taf. XIV, fig. 101; Taf. XXII, fig. 10. 1912), from the author's figures and description, represents some member of the *Penicillium frequentans* series. The name was based upon the presence of overgrowths of white mycelium, a character that is hardly diagnostic. (No one has reported the species since Sopp's work was published).

Penicillium aurantio-brunneum Dierckx (Soc. Scientif. Bruxelles **25:** 86. 1901; also, Biourge, La Cellule **33:** fasc. 1, pp. 309–311; Col. Pl. IX and Pl. XV, fig. 85. 1923) was described by Biourge as rapidly spreading, somewhat wrinkled, gray-green or blue-green to dark olive green, with colonies yellow toward reddish or orange-brown in reverse, conidiophores unbranched, with all walls smooth, conidia globose and about 3.0 to 3.5μ. Thom's observations (1930, p. 218) on Biourge's type were generally confirmatory, and he expressed the belief that the species differed sufficiently from *P. frequentans* to be fairly readily separated. Re-examination in our current study of the type strain, NRRL 766, a culture from the Centraalbureau as from Biourge, and three additional cultures previously identified as *P. aurantio-brunneum*, shows conidiophores and conidia usually finely granular and reveals no reliable bases for separation from *P. frequentans* in the broad sense that the later species is considered here.

Penicillium candido-fulvum Dierckx as described and illustrated by Biourge (Monograph La Cellule **33:** fasc. 1, pp. 275–277; Col. Pl. X and Pl. XVII, fig. 98. 1923) and as observed and reported by Thom (1930, pp. 218–219) differs little, if at all, from *P. frequentans* except for the more frequent appearance of branched conidiophores. Colonies of the type strain were reported by the latter to be broadly spreading, velvety, dull green, up to 400 to 500μ deep, umbonate in central areas, with reverse becoming yellowish to brown in age, sterigmata 8 to 10μ long, and conidia mostly 3.0 to 3.5μ (wall character not given). The type strain (NRRL 769), as maintained in this laboratory, no longer meets the colony description as given by Thom (1930) but now develops as a rather restricted, closely wrinkled, umbonate colony producing abundant conidia only in the central area; colonies and fruiting structures on malt agar, however, agree fairly well with representatives of the *P. frequentans* series. Basing judgement primarily upon earlier rather than current observations, we believe the species should be regarded as synonymous with *P. frequentans* Westling.

Penicillium columnare Thom (The Penicillia, pp. 214–215. 1930) was described as a thinly growing species which produced columnar masses of dark green conidia up to 100 to 150μ in length; conidiophores were short, about 20 to 50μ by 2.0 to 2.5 or 3.0μ and were borne on hyphae mostly submerged; conidia were about 3.0μ, faintly punctate or possibly spinulose. The strain, or strains (it was repeatedly seen during one summer's work) when isolated were regarded as meriting species recognition, but were quickly lost from the collection. In investigations since that time, strains otherwise normal have occasionally been isolated which suffer from some nutritional deficiency and which on Czapek's solution agar produce very thin growing colonies. It is believed that *P. columnare* probably represented such a strain in the *P. frequentans* series.

Penicillium flavi-dorsum Biourge (Monograph, La Cellule **33:** fasc. 1, pp. 290–291; Col. Pl. VIII and Pl. XIII, fig. 73. 1923) is regarded as closely approximating, if not duplicating, *P. frequentans* Westling. Conidiophores and sterigmata were described by Biourge as having walls squamulose and echinulate-squamulose respectively. Thom, studying the type culture (now NRRL 774), subsequently noted some markings on a part of the conidiophore walls but failed to recognize this as an unusual or distinguishing character. Conidia were reported as subglobose, about 3.0 to 3.5μ in diameter, and with a trace of pitting or echinulation. Current study of the above strain and one from the Centraalbureau, Baarn, (listed as Biourge's, but darker green and heavier sporing than NRRL 774) confirms Thom's earlier observations, but fails to provide any basis for species separation.

Penicillium fluitans Tiegs, in Ber. deut. bot. Gesellsch. **37:** 499–501. 1919. The description cites no morphology differing from members of the great *P. frequentans* series. Its chief interest lies in its unique occurrence upon or in waste water, from a munitions factory, acidified with nitric acid. Vegetative mycelium (without conidia) was reported in solutions containing 0.25N nitric acid. The organism was reported as present in pure culture under the acid conditions described and to be displaced by other species when the water was neutralized. No closer identification is possible

Penicillium glabrum (Wehmer) Westling, in Arkiv för Botanik **11:** No. 1. pp. 131–132, fig. 77. 1911; also, Thom, The Penicillia, pp. 220–221. 1930. Syn: *Citromyces glaber* Wehmer, in Beitr. z. Kennt. einh., Pilze I, p. 24; Taf. I, figs. 14–24. 1893. This species is of interest primarily from an historical point of view. Wehmer described two species of *Citromyces*, namely *C. glaber* and *C. pfefferianus*, in connection with his studies on citric acid production, but failed to differentiate adequately between them. Several years later, in a personal interview with Thom, he declined to identify either species with certainty to individual strains. The name *C. glaber* Wehmer and *P. glabrum* (Wehmer) Westling have been loosely and widely used since their inception, especially in biochemical literature, with the result that they now have even less meaning than as used by Wehmer. About all that can be said is that they usually represent strains of the *P. frequentans* series. A strain was received from the Centraalbureau, Baarn, in August 1946 bearing Westling's name which is said to have come from Thom in 1914. It apparently represents a culture received from Westling under this name and passed on to the Centraalbureau shortly thereafter. Colonies on Czapek are rapidly growing, velvety, deep dark green in color with reverse in orange-brown toward violet-red shades; conidiophores smooth or finely roughened; and conidia in compact columns, globose to subglobose, about 3.0μ with walls somewhat echinulate. The culture should be regarded as typical *P. frequentans*.

Penicillium oledzkii Zaleski (Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 499–501; Taf. 59. 1927) represents another described species properly assignable to *P. frequentans* Westling. The author's description and figures, together with Thom's observations on the type culture led the latter to this conclusion in 1930. Re-examination of the type strain, NRRL 770, as maintained in this laboratory, and as sent to us by the Centraalbureau in June 1946, fully substantiates Thom's earlier placement. The two cultures (both type) are almost indistinguishable from NRRL 1915, used as one of the centers for our diagnosis of *P. frequentans* Westling.

Penicillium pfefferianum (Wehmer) Pollacci, in Atti. Ist. Bot. Univ., Pavia, Ser. II, **16:** 121–136, Pl. XVI. 1916. Pollacci appropriates the name given by Wehmer for an organism reported as found upon rotting fruit and sausages and in solutions of sugar, citric acid, and oxalic acid. Among characteristics mentioned are conidia globose, 2.5 to 3.0μ in diameter, in solid columns, green to gray in color. There is no way to identify this mold accurately. It probably belongs with *P. frequentans* rather than *P. spinulosum*.

Penicillium sinicum Shih (Sapporo Nat. Hist. Soc. Trans. **14:** 286–287, Pl. 12, fig. 3. 1936) from the author's description appears to have been a member of the *P. frequentans* series in which the conidia were smooth, globose, 2.5 to 3.6μ in diameter, in columns up to 160μ long; conidiophores arose mostly from submerged hyphae and varied from short, 40μ, to 260μ in length.

Penicillium purpurrescens (Sopp) n. comb.

Synonym: *Citromyces purpurrescens* Sopp, in Monogr. pp. 117–119. Taf. XIV, fig. 102; Taf. XXII, fig. 4. 1912. Thom, The Penicillia, p. 178. 1930.

Colonies on Czapek's solution agar attaining a diameter of 3.0 to 3.5 cm. in 12 to 14 days at room temperature, conspicuously zonate in some strains, almost azonate in others, radiately wrinkled (fig. 50A), sometimes deeply buckled at center, consisting of a rather thick, closely-woven mycelial felt of coarse hyphae, becoming velvety or nearly so at the margin, in some strains heavily sporing throughout, in others in marginal areas only, conidial areas in dark blue-green shades near Russian to dark Russian green (Ridgway, Pl. XLII); exudate limited to fairly abundant, light amber to reddish; odor indefinite; reverse in reddish purple (R., Pl. XLIV) or brown (R., Pl. XXXIX) shades, brownish drab or dark drab (R., Pl. XLV); conidiophores generally arising in a close stand directly from the substratum (fig. 50C), mostly 100 to 150μ long by 3.0 to 3.5μ in diameter, comparatively thin walled, smooth or finely roughened, enlarging somewhat at the apices to 4.0 to 4.5μ; penicilli strictly monoverticillate as a rule, occasionally branched, bearing chains of conidia in loose columns up to 150 to 200μ long; sterigmata mostly in groups of 8 to 12, crowded in the verticil, often arising low on the sides of the vesicular area, 7 to 10μ by 2.5 to 3.5μ (fig. 50D); conidia at first elliptical, then subglobose to globose, mostly 3.5 to 4.5μ, some larger up to 5.5μ, conspicuously roughened

and showing prominent echinulations or winding color bars which may become detached when mounted in alcohol and mounting fluid.[2]

Colonies on steep agar about 4.0 to 4.5 cm. in diameter in 12 to 14 days, predominantly velvety, radiately wrinkled (fig. 50B), quickly becoming

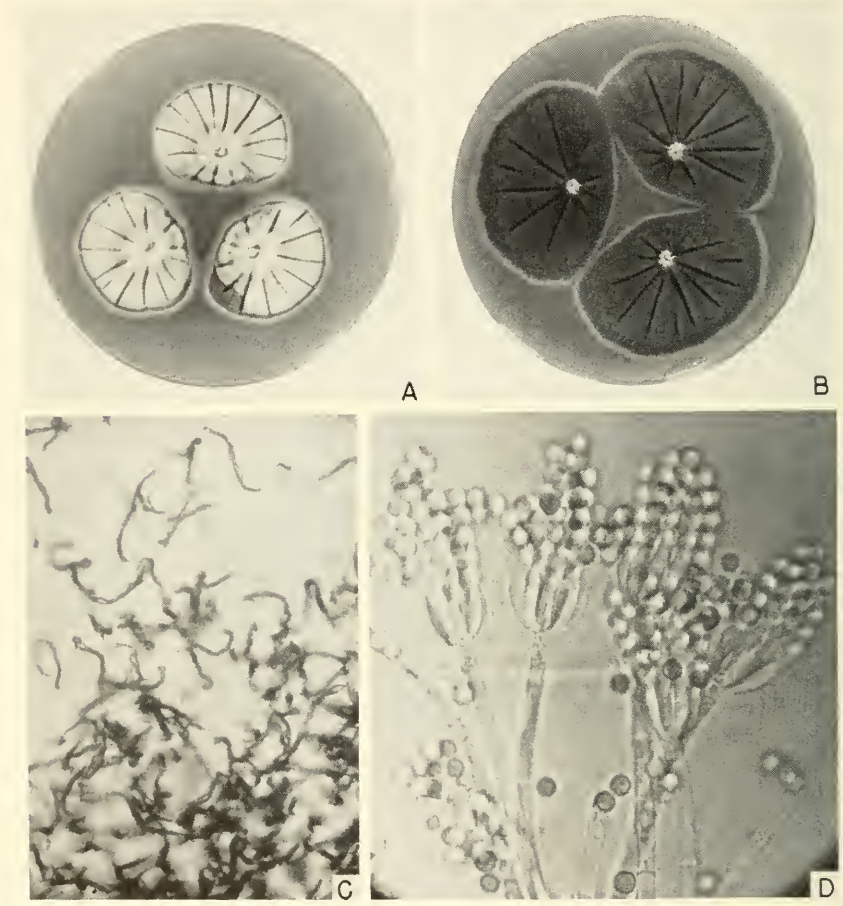


FIG. 50. *Penicillium purpurrescens* (Sopp) n. comb., NRRL 720. *A* and *B*, Two-week-old colonies on Czapek and steep agars. *C*, Low-power view of colony margin, × 40. *D*, Detail of penicilli, × 900; note echinulate globose conidia.

dull in color, approximately mouse to olive gray to dark olive gray in age (R., Pl. LI), more or less zonate; exudate limited in amount; reverse as on

[2] A similar phenomenon was reported for certain members of the *Aspergillus niger* group by Thom and Church (1926) and was regarded by Thom as probably constituting the principal basis of Lutz's smooth-walled species, *A. luteo-niger* (1907).

Czapek but darker; penicilli as on Czapek, with spore columns 100 to 200μ long, conidia somewhat more regular in size and slightly rougher.

Colonies on malt extract agar about 4.0 to 5.0 cm. in diameter in 12 to 14 days, darker near olive green to dark olive green; reverse pale but in same general shades as on Czapek; penicilli as described above but with spore columns up to 400 to 500μ long, breaking away in crusts when the culture plate is tapped.

Species description centered upon NRRL 720, a soil culture received in 1932 from Professor G. R. Bisby, University of Manitoba, Winnepeg, Canada; and NRRL 2052, received in May 1945, from Dr. W. Lawrence White, Philadelphia Quartermaster Depot, as an isolate from a leather strap in Finschafen, New Guinea. Strains showing the large globose and roughened conidia, the dark blue-green conidial areas, and the reddish purple reverse of this species are occasionally isolated from soil or soil contaminated materials. Over a period of many years, cultures showing this general morphology have come in from widely scattered sources, and *Penicillium purpurrescens*, appears to be less abundant but, like other members of the *P. frequentans* series, cosmopolitan in its distribution.

In identifying NRRL 720, NRRL 2052, and similar strains with Sopp's species, we are aware that the conidia in our cultures rarely attain the diameter of 6μ reported by him. Nevertheless, we feel justified in broadening his diagnosis (based upon a soil isolate) to include these monoverticillate forms with globose and conspicuously roughened conidia that regularly produce purple-red in reverse. There is adequate agreement between our cultures and Sopp's figures and general species description except for conidial measurements, and in this regard the disparity is not too great. We believe we can justifiably assume that the type (not seen by us) represented a unique strain, possibly some variant, showing very large conidia since among all the cultures examined by us, we have at no time encountered a strain consistently producing conidia 6μ in diameter.

A culture received from the Centraalbureau in July 1946, as *Penicillium trzebinskii* Zaleski (originally from Zaleski in 1928) fails to satisfy the description of that species, and differs from *P. purpurrescens* (Sopp) n. comb. only in producing conidial areas even darker green in color, and colony reverse in pale orange-red rather than purple-red shades. Conidia are rough-walled, irregular in form, and occasionally 5.5 to 6.0μ in diameter. The apices of sterigmata are commonly enlarged (as noted by Sopp in his *Citromyces virido-albus*) as if a conidium were continuing to grow in the absence of a bisecting wall.

A second culture received from the Centraalbureau in May 1946, as *Penicillium internascens* Szilvinyi, originally from Professor Janke in Vienna, duplicates almost exactly the description of *P. purpurrescens* as

presented above. The culture differs from NRRL 720 and NRRL 2052 primarily in producing colonies more highly colored in reverse.

Penicillium purpurrescens (Sopp) n. comb., as diagnosed above, would include the following species:

Citromyces virido-albus Sopp (Monogr. pp. 131–132, Taf. XIII, fig. 98 and Taf. XXII, fig. 12. 1912) is believed to be synonymous with *P. purpurrescens* (Sopp) n. comb. Like the latter species, *C. virido-albus* was a monoverticillate (citromyces-like) form isolated from soil which showed colony reverse in reddish to brown shades and produced large conidia 3 to 7μ in diameter with walls irregular and rough ("thorny").

Penicillium baiiolum Biourge (Monogr. La Cellule **33**: fasc. 1, pp. 305–306; Col. Pl. VIII and Pl. XIII, fig. 74. 1923) is also believed to belong with *P. purpurrescens* (Sopp) n. comb. as considered here. The species was described as a monoverticillate form producing large conidia, at first elliptical then nearly globose and rugose-echinulate when ripe. Thom's observations (1930) on Biourge's type were confirmatory. The colonies were reported to be dirty gray-green and the species was placed near the end of the section that included *P. frequentans* Westling. If Biourge's species were to be recognized, it would need to be regarded as transitional between *P. frequentans* (with smooth or finely roughened conidia) and *P. purpurrescens* (with the conspicuously roughened conidia described above). Examination of many strains assignable to these two species has failed to reveal any need for recognition of an intermediate form.

Penicillium spinulosum Thom, in U. S. Dept. Agr., Bur. Anim. Ind., Bul' 118, p. 76, fig. 32. 1910. See also Thom, The Penicillia, pp. 183–184, fig. 21. 1930.

Colonies on Czapek's solution agar growing fairly rapidly, 4.5 to 5.5 cm. in diameter in 12 to 14 days at room temperature, consisting of a loose-textured felt partially submerged, but predominantly aerial (fig. 51A), bearing conidiophores mostly as branches from loosely interlacing hyphae but commonly from submerged mycelia in marginal areas, more or less radiately wrinkled, rarely zonate, up to 1 or 2 mm. deep in central areas, heavily sporing in some strains, lightly in others (tending toward sterility under long cultivation), in dull green shades from sage green through slate olive to deep slate olive (Ridgeway, Pl. XLVII); odor very faint; exudate lacking or very limited; reverse almost colorless to light gray shades, occasionally showing a pinkish tinge; penicilli bearing spore chains in loose columns up to 100 to 150μ long; conidiophores varying in relation to their origin, usually fairly long, mostly 80 to 100μ but up to 200 to 300μ when arising from the substratum, to quite short, 25 to 50μ when arising as branches from aerial hyphae (fig. 51C), mostly 2.5 to 3.0μ in diameter, with walls almost smooth in some strains to definitely roughened in others (fig. 48C), with apices vesicular up to 5.0μ in diameter, bearing penicilli generally strictly monoverticillate but with an

occasional branch; sterigmata comparatively few in the verticil, about 6 to 10, measuring mostly 6 to 9μ by 2.2 to 3.3μ (fig. 51D); conidia subglobose to globose, rarely somewhat elliptical, mostly 3.0 to 3.5μ in diameter, definitely roughened, spinulose, or in some strains showing winding color bars.

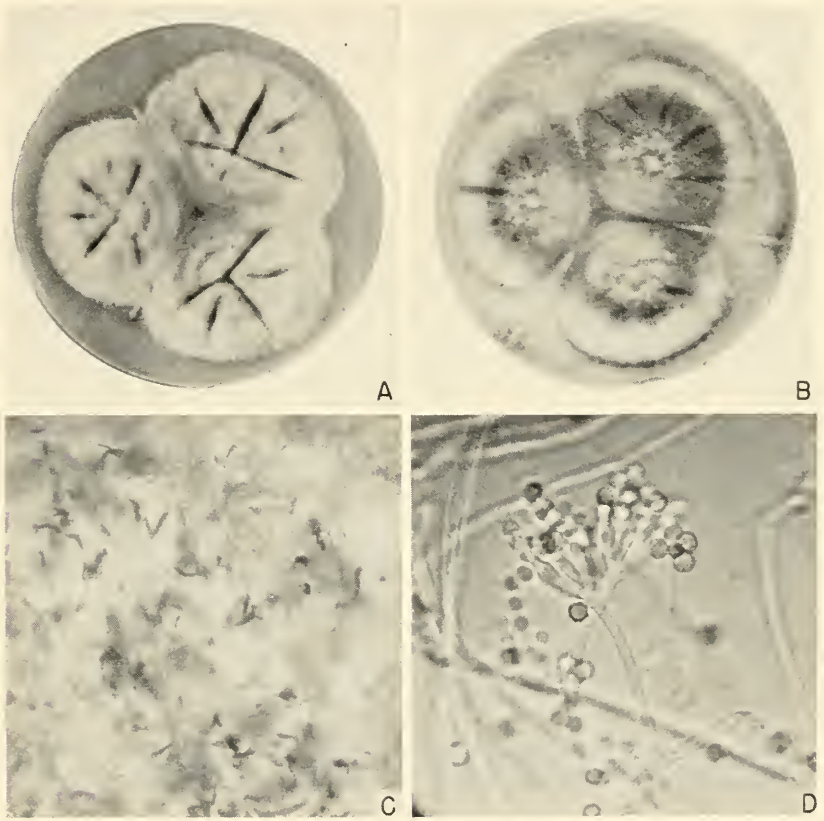


FIG. 51. *Penicillium spinulosum* Thom, NRRL 1750. *A* and *B*, Two-week-old colonies on Czapek and steep agars. *C*, Low-power views of colony surface showing penicilli commonly borne from aerial hyphae, × 40. *D*, Detail of penicilli, × 900; note spinulose character of conidial walls.

Colonies on steep agar growing more rapidly, about 6.0 to 6.5 cm. in diameter in 12 to 14 days, with mycelial felt somewhat heavier and more floccose, generally heavier sporing but in the colors listed above (fig. 51B); reverse in dull gray or drab shades; penicilli as on Czapek except sterigmata more numerous in the verticil; conidia as on Czapek but showing less irregularity in size.

Colonies on malt extract agar growing even more rapidly than on steep agar, plane, but usually showing a loose flocculent felt 2 to 3 mm. deep, heavily sporing throughout; drops numerous, enmeshed in the felt; penicilli as above but with chains of conidia showing a greater tendency to form columns.

Species description based upon Thom's notes on the type strain, his No. 45, isolated as a contaminant from a culture of another *Penicillium* obtained from Dr. Wehmer's Laboratory in Hanover, Germany, and upon observations made since that time and in the current study on a large number of strains having essentially the same cultural and morphological characteristics. NRRL 1750 may be regarded as representative. This culture stems from a transplant of Thom's No. 45 made in 1930 by Dr. H. C. Greene and subsequently maintained at the University of Wisconsin, Madison, until the spring of 1941 when it was returned to us for the NRRL Collection. Thom's type, as maintained in his collection in Washington, D. C. until 1940, and subsequently at the Northern Regional Research Laboratory in Peoria, no longer represents the species adequately. It is now essentially floccose and almost non-sporulating but still produces penicilli (usually small) and conidia characteristic of *Penicillium spinulosum*. This tendency toward sterility in strains long maintained in artificial culture is frequently encountered in this and certain other species, *e.g. P. oxalicum* and *P. purpurogenum*. The following may be listed as additional representative strains: NRRL 724 received in 1940 from Professor E. M. Gilbert, University of Wisconsin; NRRL 728 from Biourge as his *P. roseo-maculatum* (Thom No. 4733.107); and, NRRL 2051, a strain received in February 1946, from the Centraalbureau as Biourge's culture of his *P. flavo-cinereum*.

Penicillium spinulosum is world-wide in distribution and is especially common in soil, as evidenced by its frequent isolation from this source. Although confirmation has not been possible, there appears to be some evidence that this species is near, if not identical with, *Citromyces pfefferianus* Wehmer (Beitr. Kennt. Einh. Pilze I: 22–24; Taf. I, figs. 1–13. 1893).

Within the species *Penicillium spinulosum*, individual strains vary appreciably in cultural characteristics, particularly with reference to depth, general colony texture, and amount of sporulation. Strains also differ in the degree of roughness shown by conidia and conidiophores. A few strains produce conidia more or less elliptical in contrast to the usual and more typical forms with conidia globose or subglobose.

Representative strains of *Penicillium frequentans* Westling and *P. spinulosum* Thom are fairly distinct, and these can usually be identified or separated without serious difficulty. Nevertheless, strains of some-

what intermediate character are often encountered among large groups of isolates, and these tend to bridge between the two species. Such variation may occur either in colony texture and character, in details of structure, or in the colony reverse. Individual strains are placed in either one species or the other upon the basis of their more obvious relationships. Variation from *P. spinulosum* may also occur in the direction of the *P. lividum* series. *Penicillium trzebinskii* Zaleski, characterized by deeply velvety colonies and conspicuously elliptical conidia, is regarded as representing an extreme example of such variation. While this species is currently placed in the *P. lividum* series (see p. 189), its possible relationship to *P. spinulosum* is well recognized.

A number of species, more or less fully described by other investigators, are believed to belong with *Penicillium spinulosum* Thom as this species is considered here. Strain differences undoubtedly account for some of these named species. The gradations occurring within *P. spinulosum*, as it is known to us, bridge all gaps too completely to leave much hope for separation upon the bases of either cultural or morphological differences. Species reported in the literature that are believed to belong with *P. spinulosum* Thom include the following:

Penicillium (*Citromyces*) *brunneo-viride* v. Szilvinyi (Zentbl. f. Bakt. etc., (II), **103:** 145, fig. 4. 1941) was described as a fairly rapidly growing species, from almost velvety to floccose, with drops clear, hyphae smooth-walled, vesicular apices up to 5.0μ; sterigmata in simple terminal verticils, 12.5μ by 2.5μ, rather divergent; conidia globose to subglobose, about 3.7 to 3.8μ, with walls double, dark colored, and slightly roughened. There is nothing in the description to separate this species from *P. spinulosum* Thom except the heavy-walled conidia. A strain from the Centraalbureau bearing this name, originally from Professor Janke in Vienna and possibly representing the type, closely approximates *P. spinulosum* in cultural aspect and details of microscopy, but with sterigmata seldom numbering more than 6 or 7 in the verticil.

Citromyces bruntzii Sartory, in Compt. Rend. Soc. Biol., Paris **76:** 605–606. 1914. Sartory applied this name to an organism found on oranges from the Balearic Islands. The data given identifies it as monoverticillate with conidia globose 3.0 to 3.5μ in diameter and sterigmata 9 to 10μ long. Production of citric acid from glucose and a rose pigment with absorption bands near violet are reported for colonies too heavy to permit the study of individual conidiophores. The species is known only from the original description; Thom (1930) offered a guess that it might approximate *P. spinulosum*.

Citromyces citricus Mazé and Perrier, *C. tartricus* M. and P., *C. oxalicus* M. and P., and *C. lacticus* M. and P. were cited by these authors (Ann. Inst. Pasteur **18:** 558–559. 1904) in a paper on the production of citric acid by *Citromyces*. Working at the Pasteur Institute in Paris, they proposed these four names for strains of monoverticillate Penicillia isolated from organic acid solutions, as follows: *C. citricus* from a 25 percent solution of citric acid, *C. tartricus* from a 25 percent solution of tartaric

acid, *C. oxalicus* from a saturated solution of oxalic acid, and *C. lacticus* from a 4.5 percent solution of lactic acid. The observations recorded are inadequate and fail to provide separating morphological characters. They probably belong to the *Penicillium frequentans* series, but closer diagnosis is impossible.

Penicillium flavo-cinereum Biourge (Monograph, La Cellule **33:** fasc. 1, pp. 293–295; Col. Pl. VIII and Pl. XIII, fig. 76. 1923) was reported by Thom, in 1930, as belonging "in the series with *P. spinulosum* Thom". Examination of two strains received in February 1946 from the Centraalbureau bearing this name shows one to be a fairly representative culture of *P. frequentans* Westling; the other *P. spinulosum* Thom. The latter culture, now maintained as NRRL 2051, shows conidia commonly elliptical, especially as seen in chains in fluid mounts, but is otherwise typical. We do not believe adequate bases exist for maintaining Biourge's species, which undoubtedly represented a member of the *P. frequentans* series probably closest to *P. spinulosum*, as earlier indicated.

Penicillium mediocre Stapp and Bortels, in Zentbl. f. Bakt. etc., (II) **93:** 50. 1935. The authors described their organism as from the soil of a pine forest. Colonies upon wort agar spreading, bluish green to green with a broad sterile margin and scanty development of aerial hyphae; in reverse, yellow or orange at high temperatures, optimum growth at 26°C., conidiophores borne mostly as branches of aerial hyphae, rough-walled, up to 80 to 100μ long by 2 to 3μ in diameter, apices vesicle-like; sterigmata in groups of 5 to 10, definitely rough-walled, 6 to 10μ by 2 to 3μ, and conidia globose, rough, 2 to 3μ in loosely parallel chains. No data is given to separate this from *P. spinulosum*. Growth is possibly less rapid than in typical *P. spinulosum* and conidia are listed as slightly smaller.

Penicillium mucosum Stapp and Bortels, in Zentbl. f. Bakt. etc., (II) **93:** 51. 1935. The species was described as from "soil" in a beech forest, and deposited with the Centraalbureau. Our examination of the type strain, as received from Professor Westerdijk, indicates close relationship to *P. spinulosum* Thom without sufficient cultural or morphological differences to warrant continued recognition of Stapp and Bortels species. Conidia are globose, spinulose, about 2.5 to 3.0μ; conidiophores arise from the substratum and from trailing hyphae, are about 2.0 to 2.5μ wide, and are definitely roughened; penicilli are usually strictly monoverticillate, produce long parallel or tangled chains of conidia rarely in well defined columns; colonies in reverse show dull reddish purple shades suggestive of *P. purpurrescens*.

Citromyces pfefferianus Wehmer, in Beitr. z. Kenntn. einheim. Pilze **I:** 22–24; Taf. I, figs. 1–13. 1893. Wehmer found his organism on rotting fruits of *Citrus medica* and cited it as the agent of citric acid production in his patent. Morphological data as given might indicate any one of many strains of monoverticillate Penicillia. Verified cultures were never distributed. By 1905, so many monoverticillate forms had been cultivated that he acknowledged that he could no longer recognize either of his two original species. There is persistent belief that *C. pfefferianus* was some member of the species aggregate now designated as *Penicillium spinulosum*.

Penicillium pfefferianum (Wehmer) Westling, in Arkiv för Botanik **11:** 132–133. 1911 (also in Biourge's Monograph, La Cellule **33:** fasc. 1, pp. 303–305; Col. Pl. VIII and Pl. XII, fig. 72. 1923). Biourge attributes to Westling a strain which is now contained in our collection as NRRL 727, brought by Dr. Paul Simonart from Biourge's Laboratory. It shows the morphology of this group, but produces deep dark

green, close-textured, strongly wrinkled colonies on Czapek with reverse and media in dull violet-red shades. Conidia and conidiophores are rough. It is assigned to *P. spinulosum* Thom in the *P. frequentans* series.

Penicillium roseo-maculatum Biourge (Monograph, La Cellule **33:** fasc. 1, pp. 301–303, Col. Pl. VIII and Pl. XII, fig. 71. 1923), as suggested by Thom in The Penicillia (1930, p. 186), should be regarded as *P. spinulosum* Thom. Thom's notes made prior to 1930, and our observations made during the present study on Biourge's type (now NRRL 728) furnish no bases for recognition of a separate species. Colonies show considerable aerial growth in masses up to 0.5 to 1.0 mm. deep, conidial areas in dull blue-green shades, conidiophores loosely ascending, bearing simple verticils of sterigmata and chains of conidia in columns up to 100μ or more; conidia with walls faintly spinulose, globose or nearly so, about 3μ in diameter.

Penicillium viridi-dorsum Biourge (Monograph, La Cellule **33:** fasc. 1, pp. 306–307; Col. Pl. VIII and Pl. XIII, fig. 75. 1923) was described and figured as a monoverticillate form producing blue-green to gray-green conidial areas, colonies toward reddish or hyacinth in reverse, conidiophores smooth and conidia globose, granular or echinulate, 3.0 to 4.5μ. Studying the type strain, Thom (1930, pp. 186–187) reported colonies up to 500μ deep with conidiophores tangled, or ascending from creeping or partially submerged hyphae, colorless below, and conidia as 2.5 to 3.0 or 3.5μ in diameter and with walls smooth or showing traces of wrinkles. Reexamination of the type (now NRRL 730) in our current study is generally confirmatory but shows conidia to be delicately and consistently spinulose. There are no grounds for separation from *P. spinulosum* Thom.

Penicillium tannophagum Stapp and Bortels (Zentbl. f. Bakt. etc. (II) **93:** 52. 1935) was reported to break down tannin in a 5 per cent solution, hence the name. It was described as rather slowly spreading on wort agar, velvety, with scattered aerial hyphae, green with margin bluish; reverse in yellowish or orange shades; conidiophores smooth, from 40 to 80μ long if borne as branches from aerial hyphae, 100μ long if arising from the substratum, 2.5 to 3.0μ in diameter, with apices swollen to about 5.0μ; sterigmata in simple verticils of 8 to 12, measuring 8 to 10μ by 2.5 to 3.0μ; conidia round, slightly roughened, in loosely parallel more or less adherent chains. By description the species would be assignable in the *P. frequentans* series. Examination of the type strain received from the Centraalbureau in 1946 showed a culture agreeing with the original description in general characteristics but failing to show sufficient differences from *P. spinulosum* Thom to warrant species recognition.

Penicillium tannophilum Stapp and Bortels (Zentbl. f. Bakt. etc. (II) **93:** 52. 1935) was reported to break down tannin in concentrations up to 20 per cent. It was described as felted, dark green, zonate, rather slow growing on wort agar with reverse colorless; conidiophores mostly arising from the substratum, about 100μ by 2.8 to 3.2μ, swelling at the apex; sterigmata in simple verticils of 7 to 10, measuring 9 to 10μ by 3.0 to 3.5μ; conidia smooth or weakly roughened, in loose parallel chains (columns ?) or tangled, slightly elliptical, 3.2 to 3.8μ by 2.8 to 3.0μ. Examination of the type, contributed by the Centraalbureau in 1946, is generally confirmatory but shows colonies growing rather rapidly on all media, with reverse in orange to reddish brown shades. The total cultural picture is that of a member of the *P. frequentans* series strongly suggestive of *P. frequentans* Westling, but the character of the conidia seem to indicate closer affinities to *P. spinulosum*. The strain shows distinct characteristics but is not regarded as warranting separation from the latter species.

Occurrence and Significance

Pennicillum frequentans Westling and *P. spinulosum* Thom are two of the most abundant and widely distributed members of the monoverticillate Penicillia. *Penicillium purpurrescens* (Sopp) n. comb. is somewhat less common. Members of this series typically represent soil fungi and in our experience constitute a normal component of the mycoflora of all soils examined. Like many other soil fungi, and in greater abundance than most, they occur in nature under a wide range of conditions and upon a great diversity of substrata. They may be found upon almost any type of organic material which is undergoing slow aerobic decomposition. A few references will serve to illustrate this range. *Penicillium spinulosum* was one of the species most commonly isolated by Snow (1945) from oats, linseed cake, and palm kernel cake stored at 75 percent to 100 percent R.H. Gopp, Christ, and Reich (1937) reported *Citromyces pfefferianus* Wehmer (= *P. spinulosum* Thom of this Manual) as one of a group of fungi causing extensive mold growth and impairment of aroma in stored hops. Ullscheck (1928) reported *P. spinulosum* to represent one of nine types of *Penicillium* commonly encountered in the cheese cellar. Grimes, *et al.* (1930) found *P. spinulosum* to be generally present in butter although no special significance was attributed to it. In testing various fungicides for their efficacy in "tropic-proofing" optical instruments, Turner, *et al.* (1946) cited *P. spinulosum* as one of the molds commonly isolated from such instruments in New Guinea, and in our experience it was commonly encountered among cultures isolated from materiel and submitted to us for identification. Richter (1931) reported species of *Citromyces* without further identification, but probably belonging to this series, to be responsible for mustiness in seed grain. James, Wilson, and Stark (1946) reported *P. spinulosum* as one of the molds commonly identified in the flora of stored wheat. Passmore (1931) identified *P. candido-fulvum* Dierckx (= *P. frequentans* Westling of this Manual) among the molds isolated from, and responsible for, the spoilage of prepared copra. *Penicillium frequentans* was used by Hoffman, *et al.* (1940) to assay the fungistatic properties of acetic and proprionic acids in which chlorine substitutions had been made.

A possible role of the above forms in decay processes in nature is indicated by their ability to decompose tannin. Rippel and Keseling (1941) reported species of *Penicillium*, *Citromyces*, and *Aspergillus* to be able to utilize tannin as a source of carbon. Tannase was produced only in the presence of tannin but was not associated with the ability of the mold to utilize this substance. Stapp and Bortels (1935) found a number of molds belonging to the present series to be capable of growing in concentrated tannin liquors. Two new species, *Penicillium tannophagum* and *P.*

tannophilum, were described and named because of their ability to decompose tannin rapidly. Two additional new species, *P. mucosum* and *P. mediocre* were also found to break down tannin. All of these species approximate *P. spinulosum* Thom, and are so regarded in the present Manual.

Limited study has been devoted to the production of enzymes by members of this series. From a blue-green *Penicillium* referred to as *P. glaucum*, Kertesz (1928) reported sucrase production to be directly proportional to the amount of sucrose in the substrata in concentrations of from one to 30 percent. No sucrase was formed in an invert sugar medium, and raffinose gave yields almost equal to sucrose. Formation of the enzyme was thus regarded as dependent upon the presence of an α-fructoside grouping in the nutrient medium. Methods for determining the amounts of invertase in the mycelium of a mold and in the culture medium were subsequently published by the same author (1931), at which time he reported that enzyme production increased with increased sugar concentration only in the presence of adequate potassium, phosphorous, and magnesium. Kertesz further (1930) reported the production of a pectin decomposing enzyme, pectinase, by *P. glaucum*, which was subsequently identified by Thom as *P. frequentans* Westling and cited in this Manual as NRRL 763 (see p. 174). An enzyme preparation derived from this mold was successfully used to clarify cider and other fruit juices. The preparation had an optimum acidity of pH 3.0 to 3.5 and an optimum temperature of 40° C. and was completely inactivated by heating at 55° C. for 30 minutes. The addition of 0.5 percent enzyme solution was sufficient to completely clarify cider in 13 hours at 25° C. Williman and Kertesz (1931) presented additional information regarding the concentration and use of a pectin dissolving enzyme paying particular attention to its practical application for the clarification of grape juice. In this paper, the responsible enzyme was reported to be different from either pectinase or pectase. Studying the saccharification of Jerusalem artichokes by mold inulases, Asai (1937) reported 7 varieties of *Citromyces* to be active producers of this enzyme. Alvik (1931) studied the production and stability of mold diastases elaborated by members of the *P. glabrum* series but failed to include any quantitative data regarding production. Horowitz-Vlassova and Livschitz (1935) reported certain fungi, including *C. pfefferianum* (probably *P. frequentans*) to be able to disintegrate fats and oil by oxidation. Fungal lipase and an oxidation-inducing enzyme termed lipoxidase could not be detected in the substrate but could be found in the mycelium.

Some interesting metabolic products are known to be produced by members of the series. Anslow and Raistrick (1938a) identified 3,6-dihydroxy-4-methoxy-2,5-toluquinone in cultures of *Penicillium spinulo-*

sum, and applied to it the name spinulosin. The substance was subsequently identified from *Aspergillus fumigatus* and later synthesized by the same investigators (1938b and c). Raistrick in the same year reviewed the production by molds of spinulosin and other quinones, including fumigatin, a metabolic product of *Aspergillus fumigatus* Fres. Evaluating the possible antibiotic activity of spinulosin, Oxford (1942b) and Oxford and Raistrick (1942) found it to have relatively low antibacterial activity, inhibiting Gram-positive and gram-negative forms only at dilutions of 1:20,000. It is of no particular interest as a possible therapeutic agent.

Hetherington and Raistrick (1931) reported a yellow coloring matter to be produced from glucose by various species of *Citromyces*, including *C. glaber* and *C. pfefferianus* (regarded as probably *Penicillium frequentans* and *P. spinulosum*, respectively). The pigment was designated citromycetin ($C_{14}H_{10}O_7$) and its detailed characterization published. It is almost insoluble in cold water, slightly soluble in hot water, somewhat soluble in acetone, fairly soluble in cold absolute alcohol and in hot glacial acetic acid, and readily soluble in aqueous Na_2CO_3 and $NaHCO_3$ with the evolution of CO_2. It can be crystallized from 50 percent aqueous ethanol as lemon yellow needles containing two molecules of water of crystallization.

Krocker, Strong, and Peterson (1935) investigated the lipids of *Penicillium aurantio-brunneum* (regarded as *P. frequentans* in this Manual) and found them to consist essentially of glycerides of palmitic, stearic, oleic, and linoleic acids. Ergosterol was isolated from the non-saponifiable matter.

The capacity to produce citric acid appears to be fairly common to members of the *Penicillium frequentans* series, although in no case are yields known to equal those obtained with selected strains of *Aspergillus niger*. The production of citric acid by molds which are now recognized as belonging to this series was first reported by Wehmer in 1893. He created a new genus, *Citromyces*, and described two new species, *C. glaber* and *C. pfefferianus*, to incude the responsible strains. His patents taken out in Germany (1894), France (1893), Britain (1893), and the United States (1894), were based upon their use. While positive confirmation is impossible, a sufficient continuity of correspondence and observations exists to support the belief that Wehmer's species approximated *P. frequentans* Westling and *P. spinulosum* Thom as we now know them. Mazé and Perrier (1904) investigated citric acid production in *Citromyces* and described four new species as follows: *C. citricus*, *C. tartricus*, *C. oxalicus*, and *C. lacticus*.

Butkewitsch (1925) investigated conditions favoring the formation of gluconic and citric acids by *Citromyces glaber* and *Penicillium glaucum*,

and reported that a low acidity favored the formation of the former, whereas a high acidity favored formation of the latter acid. Chrzaszcz and Tiukow (1929) investigated citric acid formation by forty-six species of Penicillia, including strains of *C. glaber* and *C. pfefferianus*, and reported citric acid to be produced by all but three, with the quantity largely dependent upon the species. Particular attention was devoted in later papers to the production of acid by a strain designated *Penicillium "X"*, n. sp., and referred to as a citric acid producing organism belonging in the section Aspergilloides, but was not otherwise identified. Mechanisms for the production of citric acid by mold fermentations were proposed by Chrzaszcz and Tiukow, in 1930 and 1932. Oxalic acid production by *Penicillium "X"* was also investigated by these authors (1930a). Filosofov and Malinovskii (1928) reported *Citromyces* to produce citric acid equal to 17.1 percent of the sugar in the substrate in 20 days. Frey (1931) compared citric acid production in *Aspergillus niger* and *C. glaber*, and found the fermentation by the latter to be adversely affected by pH 2.0 produced by mineral acids, whereas *A. niger* was not so inhibited. Birkinshaw and Raistrick (1931) reported certain strains of *P. spinulosum* to produce good yields of citric acid.

Penicillium lividum Series

Outstanding Characters

Colonies usually appearing deeply velvety to lanose, consisting of a tough basal felt having abundant conidial structures, with conidia in definite blue-green shades.

Conidiophores typically erect or ascending, long, usually unbranched with walls often finely roughened and with apices somewhat enlarged.

Penicilli strictly monoverticillate with sterigmata usually crowded in the verticil, parallel or somewhat divergent.

Conidia elliptical to subglobose, mostly 3.0 to 4.0μ in long axis, with walls echinulate, often conspicuously so.

Series Key

1″. Colonies deeply lanose, conidiophores 400 to 500μ or more in length, reverse uncolored or in fairly light shades.

aaa. Conidia broadly elliptical to ovate, conspicuously roughened *P. lividum* Westling

bbb. Conidia narrowly elliptical with ends pointed, delicately roughened *P. aurantio-violaceum* Biourge

2″. Colonies not deeply lanose, conidiophores comparatively short, reverse in deep violet to violet-black shades, conidia spinulose..... *P. trzebinskii* Zaleski

Members of this series represent a normal component of the mycoflora of most soils, but occur less frequently than most of the other recognized

monoverticillate forms. The series contains three well-marked species. *Penicillium lividum* Westling is easily recognized by its deep velvety colonies, its typical blue-green color, and its rough-walled, broadly elliptical to ovate conidia. *Penicillium aurantio-violaceum* Biourge presents much the same cultural picture but differs markedly in producing strongly elliptical conidia with ends usually somewhat pointed. *Penicillium trzebinskii* Zaleski is characterized particularly by the production of colonies with reverse in deep dull violet to fuscous shades. The series appears to be closely related to the *P. frequentans* series through a *P. trzebinskii* to *P. spinulosum* bridge (see p. 183).

Penicillium lividum Westling, in Arkiv för Botanik **11:** 58, 134–137, fig. 79. 1911. See also Dale, Ann. Mycol. **12:** 52. 1914; and Thom, The Penicillia, pp. 205–206. 1930.

Colonies on Czapek's solution agar growing fairly rapidly, approximately 3.0 to 3.5 cm. in 10 to 12 days at room temperature, lightly furrowed (fig. 52A), about 1 mm. deep, consisting of a tough basal felt with loose surface growth, deeply velvety to almost lanose, azonate or nearly so, at first white but showing blue to blue-green shades with the development of abundant conidial structures after 6 to 8 days, ranging progressively from glaucous gray to grayish blue-green (Ridgway, Pl. XLVIII) to approximately deep olive to dark olive gray in age; exudate lacking; odor wanting or indefinite; reverse at first uncolored, becoming dull peach to flesh shades in age; conidiophores mostly single and arising from the substratum separately, usually unbranched but occasionally with a branch somewhat below the tip, long, up to 400 to 600μ or more by 2.5 to 4.0μ (fig. 52C), septate, smooth-walled or nearly so, swelling somewhat at the apex and sometimes truly vesicular up to 5.0 to 6.0μ in diameter; penicillus usually consisting of a single verticil of parallel or somewhat divergent sterigmata bearing tangled conidial chains up to 50μ or more in length, rarely forming loose columns; sterigmata mostly 5 to 10 in the verticil, 8 to 12μ by 2.0 to 3.0μ, occasionally 15μ in length, with fairly conspicuous spore-bearing tips (fig. 52D); conidia at first definitely elliptical, in age usually becoming ovate to subglobose, mostly 3.0 to 4.0μ by 2.6 to 3.0μ, with walls clearly roughened and commonly showing definite spiral banding, especially in larger and more elliptical cells.

Colonies on steep agar growing more rapidly, up to 5.0 to 5.5 cm. in 10 to 12 days, lightly furrowed or plane, with composition and texture as on Czapek, deeply velvety or lanose with loose aerial growth 1.0 mm. or more deep (fig. 52B), medium to heavy sporing throughout except for a narrow, white growing margin 1.0 to 2.5 mm. wide, conidial areas colored as on Czapek; conidiophores arising almost exclusively from the substratum or

the basal felt, smooth-walled, commonly 500 to 800μ or more in length, sometimes branched but bearing strictly monoverticillate penicilli averaging slightly larger than on Czapek; conidia more commonly remain elliptical at maturity, otherwise, as described above.

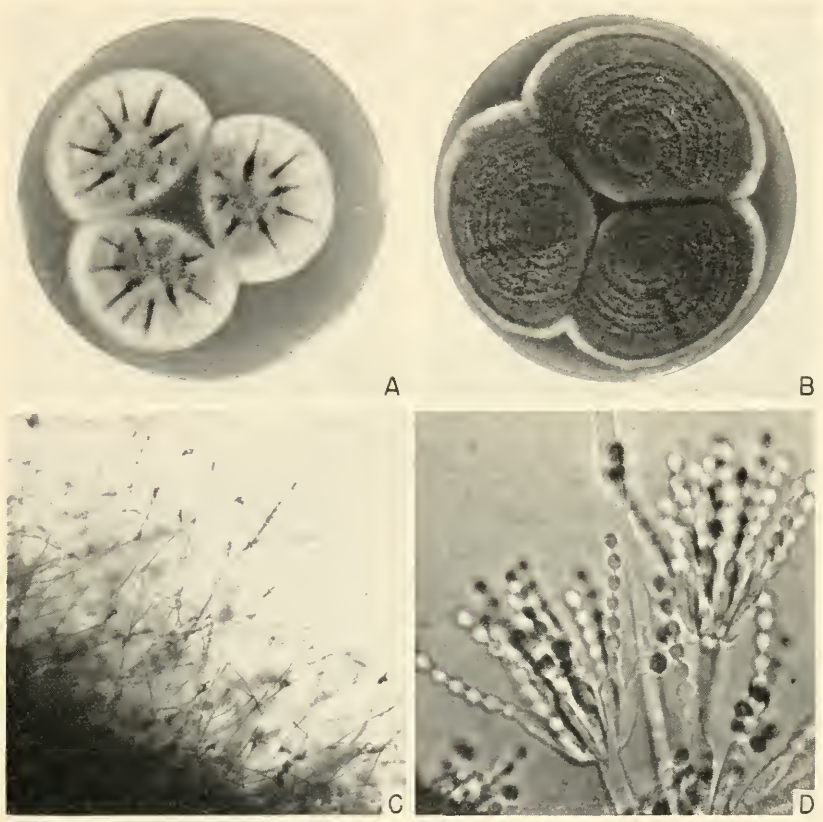


FIG. 52. *Penicillium lividum* Westling, NRRL 754. *A* and *B*, Two-week-old colonies on Czapek and steep agars. *C*, Low-power view of colony margin showing characteristic long conidiophores, × 40. *D*, Detail of penicilli, × 900.

Colonies on malt agar growing rapidly, up to 5.0 to 6.0 cm. in 10 to 12 days, not furrowed, very loose textured, deeply velvety to lanose, 2 to 3 mm. deep, heavily sporing in colony centers, thinning outward, with denser conidial areas ranging from dark glaucous gray to grayish blue-green (R., Pl. XLVIII) to deep grayish blue-green in age; no odor or exudate; reverse in orange shades; conidiophores originating as above but commonly up to 1 mm. or more in length and with walls often finely

roughened in terminal and subterminal areas; penicilli and conidia as on steep agar.

Westling's type strain was reported from stored root-stock of *Polystichum filixmas* and grew well upon common media. The type was lost by Westling before his cultures were sent to Thom in 1911. A second culture, Thom's number 2697, however, was received from Miss Dale in Scotland in 1913 and identified by Thom as *Penicillium lividum*, then sent to Westling who verified the identification. This latter culture is maintained in our Collection as NRRL 754. It constituted the principal basis for Thom's redescription of Westling's species in 1930, and for the current diagnosis as presented here.

Penicillium lividum Westling, while less abundant than many species, is not infrequently encountered among isolates from soil, from stored cereal products, and from other organic materials subject to air or soil borne contamination. The species is apparently cosmopolitan in distribution.

Culture NRRL 2062 received from the Centraalbureau in June 1946, labelled *Penicillium lividum* Westling, and in an accompanying letter noted as having come from Thom in 1930, differs from the above description in producing comparatively thin, close-textured, strongly restricted colonies, about 1.0 to 1.5 cm. wide on Czapek's solution agar in 10 to 12 days, with short conidiophores rarely more than 50 to 100μ in length, heavily sporing over the whole surface, in blue-green shades near bluish gray-green or deep bluish gray-green (R., Pl. XLII). In colony characteristics, this strain fits *P. lividum* only in the color of conidial areas. The penicillus, however, agrees quite well with that described for NRRL 754 and commonly shows even larger clusters of sterigmata borne on enlarged conidiophore apices up to 6.0μ or more in diameter. Conidia are likewise typical of the species, being broadly elliptical, about 3.5 to 4.5μ by 3.0 to 3.5μ with walls conspicuously roughened. The strain from the Centraalbureau cannot be regarded as representing the species satisfactorily; however, it cannot be removed from it because of the conidial structures produced.

Penicillium aurantio-violaceum Biourge, in Monogr., La Cellule **33:** fasc. 1 pp. 282–284; Col. Pl. X and Pl. XVI, fig. 94. 1923. Also in Thom, The Penicillia, p. 208. 1930.

Colonies on Czapek's solution agar growing rapidly, attaining a diameter of 4.0 to 4.5 cm. in 10 to 12 days, plane or lightly furrowed, azonate or slightly zonate (fig. 53A), comparatively deep up to 1.5 mm. in colony centers, consisting of a tough mycelial felt at the agar level with surface growth loose, deeply velvety to lanose, consisting primarily of long ascending conidiophores. Growing margin broad and rather thin, heavily spor-

ing throughout in light blue-green shades near pea green to celandine green (Ridgway, Pl. XLVII), remaining approximately unchanged in age; exudate lacking; odor slight, somewhat peculiar, but not distinctive; reverse at first in cream to dull yellow shades changing to quaker-drab in age; conidiophores abundantly produced, arising primarily from sub-

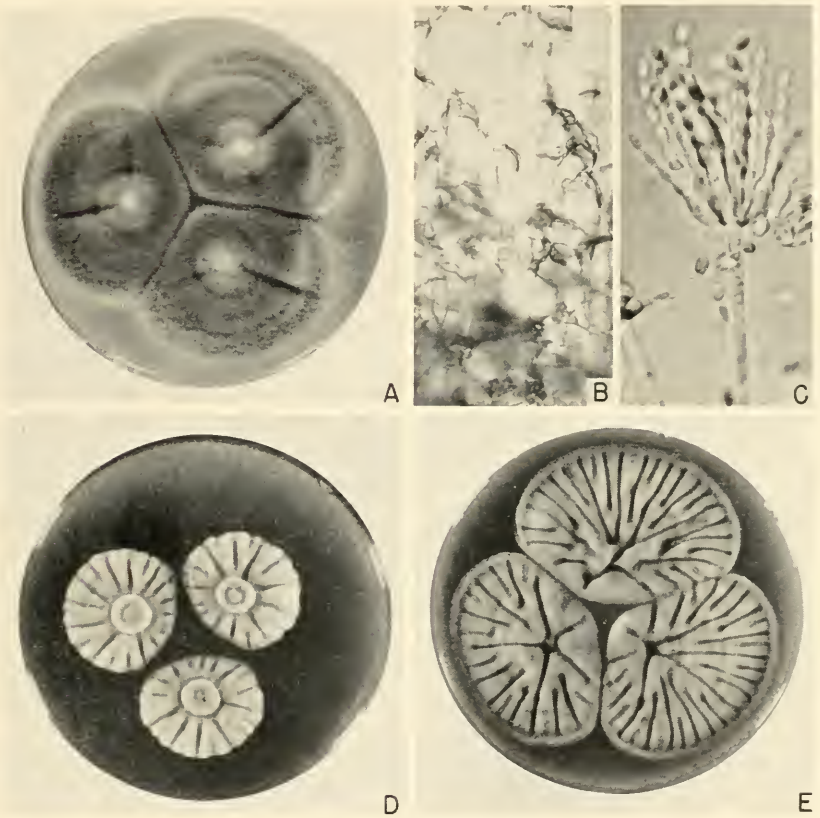


FIG. 53. *A–C*, *Penicillium aurantio-violaceum* Biourge, NRRL 760. *A*, Two-week-old colony on Czapek agar. *B*, Low-power view of colony margin showing long conidiophores, × 40. *C*, Detail of penicillus, × 900. *D* and *E*, *P. trzebinskii* Zaleski, NRRL 731, growing upon Czapek and steep agars.

merged hyphae or from the basal felt, long, ascending, becoming somewhat tangled, up to 400μ or more in length by 2.5 to 3.5μ (fig. 53B), occasionally branched, walls closely and finely echinulate, apices somewhat enlarged up to 4.5 to 5.0μ; penicilli strictly monoverticillate and consisting of closely crowded verticils of 8 to 12 or more sterigmata with tips somewhat divergent, bearing parallel or divergent conidial chains up to 100μ or

more in length; sterigmata about 8 to 10μ by 2.0 to 2.5μ with conidium bearing tips definitely narrowed (fig. 53C), conidia strongly elliptical, almost fusiform, about 3.0 to 3.5μ by 2.0 to 2.5μ, with ends usually somewhat pointed and with walls delicately roughened, sometimes appearing smooth.

Colonies on steep agar as above but generally somewhat deeper and regularly heavier sporing, uniformly colored throughout, approximately pea green (R., Pl. XLVII) to storm gray (R., Pl. LII); odor and exudate lacking; reverse in light drab shades; conidial structures as described on Czapek but with conidiophores commonly more than 500μ in length and conidial chains up to 200μ; details of the penicillus as above.

Colonies on malt agar spreading broadly, 6 to 7 cm. in 10 to 12 days, comparatively deep, loose-textured with growing margin broad, white, about 5 mm., light gray-green near gnaphalium green to pea green (R., Pl. XLVII), remaining essentially unchanged in age; reverse in dull yellow-orange shades; conidial structures as described above.

Species diagnosis centered upon a strain isolated by Stapp and Bortels (1935) from a beech forest in Berlin and used as the type of their new species, *Penicillium rosco-viridum*. It is now maintained as NRRL 760. A second substrain of the same culture, received from the Centraalbureau in August 1946, duplicates NRRL 760. When first examined in 1936, Thom recognized Stapp and Bortel's strain as unquestionably representing *P. aurantio-violaceum* Biourge, hence considered their species as synonymous with that earlier described by Biourge.

NRRL 762, received in 1940 from Professor R. A. Toro, University of Puerto Rico, Mayaguez, P. R., differs from the above in producing colonies consistently more floccose, with appreciable sterile hyphae, and with more strongly roughened conidiophores. The structure of the penicillus and the size and shape of the conidia duplicate NRRL 760 as discussed above.

Penicillium trzebinskii Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat., Ser. B, 1927, pp. 489–499; Taf. 58. Thom, The Penicillia, p. 189. 1930.

Colonies on Czapek's solution agar attaining a diameter of 2.0 to 2.5 cm. in 10 to 12 days at room temperature, consisting of a tough basal felt with thin aerial growth appearing almost floccose, strongly and irregularly wrinkled and somewhat radially furrowed, azonate (fig. 53D), light to medium sporing throughout, in pale gray-green shades from an admixture of conidial heads and sterile aerial hyphae; no exudate produced; odor lacking or indefinite; reverse quickly developing deep dull violet to dark fuscous shades, with surrounding agar similarly colored; conidiophores limited to abundant, sometimes arising from submerged hyphae,

more commonly from the aerial mycelium or from the basal felt, variable in length up to 150 to 200μ by 1.8 to 2.5μ in diameter, mostly unbranched, with walls delicately but conspicuously echinulate; penicilli strictly monoverticillate, generally small, with sterigmata in verticils of 4 to 6 or 8, rarely more (Zaleski reported up to 20 or 25 upon neutral Raulin-gelatin); sterigmata about 8 to 10μ by 1.8 to 2.2μ, parallel, with conidium-bearing tips definitely narrowed; conidia broadly elliptical to subglobose, mostly 2.5 to 3.3μ in long axis, with walls conspicuously echinulate.

Colonies on steep agar growing more rapidly, up to 4.5 to 5.0 cm. in 10 to 12 days, strongly wrinkled in a cerebriform manner, in texture as on Czapek but somewhat heavier sporing (fig. 53E), becoming dull gray-green in age; exudate limited, clear to pale yellowish; reverse as on Czapek but developing dark shades less rapidly; conidiophores longer, commonly up to 300 to 400μ; penicilli somewhat larger and with conidia in adherent, loosely parallel chains often forming irregular columns up to 100μ or more in length.

Colonies on malt agar spreading, up to 5 cm. in 10 to 12 days, loose-textured, almost floccose and 1 to 2 mm. deep, not furrowed or wrinkled, reverse uncolored or in pale golden shades, medium sporing throughout, conidiophores arising primarily from aerial hyphae, criss-crossed in the manner of *Penicillium spinulosum*, commonly 200 to 300μ or more in length by 2.0 to 2.5μ in diameter, with apices inflated up to 4.0 to 4.5μ and with walls conspicuously echinulate; sterigmata crowded, up to 10 or 12 in the verticil, otherwise as described on Czapek, bearing conidia in loose columns up to 150μ or more in length.

Species description based primarily upon Zaleski's type, isolated from forest soil in Poland. This culture received from the Centraalbureau in 1928 and now maintained as NRRL 731, was discussed by Thom in his Monograph (1930, p. 189) as No. 5010.27. NRRL 2073, isolated from lettuce seed and sent to us in January 1945 for diagnosis by J. Walton Groves, Central Experimental Farm, Ottawa, Canada, is considered as representing *Penicillium trzebinskii* but differs from the type in certain details. Colonies are heavier sporing, develop less purple color in reverse, penicilli are generally somewhat larger, and conidia are definitely elliptical but less conspicuously echinulate than those of NRRL 731.

Some additional cultures showing conidiophores and conidia echinulate and reverse in purplish to violet shades have been encountered, and the proper placement of *Penicillium trzebinskii* remains somewhat questionable. It is placed with the *P. lividum* series, since it produces long, rough conidiophores and echinulate conidia that are usually broadly elliptical. The over-all picture of the species, however, suggests close relationship to *P. spinulosum* Thom and it is possible that the latter species should be

broadened sufficiently to include it. Strains showing progressive gradation between the *P. frequentans* and the *P. lividum* series have been examined. Representative of such strains is a soil culture received from the Centraalbureau in June 1946, as the type of *P. mucosum* Stapp and Bortels. The latter species is regarded as belonging with *P. spinulosum* (see p. 184).

The conidia of NRRL 731 are typically broadly elliptical, although, in some cultivations, many appear subglobose. Some difficulty may be experienced in locating the species in the *Penicillium lividum* series for this reason. It is hoped that the examination of additional closely related strains will, in time, enable us to establish the true relationships of *P. trzebinskii*.

Occurrence and Significance

Penicillium lividum Westling and allied species occur rather infrequently among soil isolates but are believed to be widely distributed. Their role in decomposition processes is unknown but is regarded as probably insignificant. Bouriquet (1941) isolated *P. lividum*, *P. rugulosum*, *Aspergillus niger*, and a new species, *P. vanillae*, from vanilla undergoing spoilage in Madagascar. Mold damage was most prevalent at the base of the fruits, an area relatively poor in vanillin. Growth of each of the above molds was checked by a concentration of 1 percent vanillin when added to a nutrient solution. Stapp and Bortels (1935) reported *P. roseo-viridum* to break down tannin in concentrations of 5 to 50 percent.

Penicillium implicatum Series

Outstanding Characters

Colonies growing restrictedly upon most substrata, usually compact, velvety, heavy sporing, mostly in blue-green shades; vegetative mycelium sometimes encrusted and pigmented, characteristically producing conspicuous orange-red to maroon colors in colony reverse.

Penicilli strictly monoverticillate, usually borne upon conidiophores arising from the substratum or from a compact basal felt, erect, seldom branched, variable in length, commonly less than 200μ, but in some strains 300 to 400μ, with apices usually inflated and appearing somewhat vesicular.

Chains of conidia long, loosely parallel or adherent, often forming fairly well developed columns, crowded in most strains and often tending to break away as crusts in old cultures.

Conidia smooth or delicately roughened, elliptical to subglobose or even globose, from 2.0 to 2.5μ in some strains to 4.0 or 5.0μ in others.

Series Key

b. Colonies growing rather restrictedly upon most media, especially Czapek's solution agar ..... *P. implicatum* series

1′. Conidial areas light blue-green, colony reverse in bright orange-red or red shades, conidia globose to subglobose, in parallel or divergent chains
P. multicolor G.-M. and P.

2′. Conidial areas commonly deep blue-green, colony reverse in orange-brown or maroon shades, conidia broadly elliptical, usually in compact columns
P. implicatum Biourge

3′. Conidial areas yellow-green to gray-green, reverse in orange-red shades (approaching brick red), conidia strongly elliptical or pyriform
P. sublateritium Biourge

The *Penicillium implicatum* series represents an aggregation of strains, not identical in details of structure or reactions, but having much in common and grading into one another sufficiently to justify grouping them together. Three species are recognized, namely: *P. implicatum* Biourge, *P. multicolor* Grigorieva-Manoilova and Poradielova, and *P. sublateritium* Biourge.

Of these species, the first is by far the most abundant and the most variable. Thom (1930, p. 211) recognized this variability by presenting a series description covering Biourge's type and additional strains obviously closely allied to it. In the present discussion we have enlarged still further the *Penicillium implicatum* series concept, with the characteristics outlined above, and have incorporated into the specific diagnosis the general range of characters formerly attributed to the series. The species *P. implicatum* is characterized particularly by its restricted growth, velvety surface, heavy spore (conidium) production, deep blue-green color, and the development of deep orange-red to maroon shades in the colony reverse and the surrounding medium.

Penicillium sublateritium Biourge possesses the basic characteristics of *P. implicatum* but differs from that species in developing colonies that run to gray-green rather than blue-green shades and in producing relatively large conidia up to 4.0 to 5.0μ in long axis.

Penicillium multicolor G.-M. and P. is clearly distinct and once studied in culture is easily recognized. It is characterized particularly by the production of yellow to orange or orange-red vegetative mycelium and bright orange-red to scarlet shades in reverse. Unlike *P. implicatum*, the pigmentation does not extend into the surrounding agar; conidia are in lighter blue-green shades, and conidial chains, while mostly parallel, are not adherent into definite columns.

Members of this series occur regularly in and are fairly abundant upon substrata subject to soil or dust borne contamination. *Penicillium implicatum* is especially common.

Pennicillium multicolor appears twice in the Monoverticillata Key. Cultural characteristics and details of structure place it in the *P. implicatum* series, but its tendency to grow rather rapidly upon steep agar and other substrata containing vegetable extracts necessitates keying it with the *P. frequentans* series also.

Penicillium multicolor Grigorieva-Manoilova and Poradielova, in Archives des Sciences Biologiques Leningrad **19:** 117–131, fig. 1 and one plate with photographs 1–6. 1915 (in Russian). Thom, The Penicillia, pp. 212–213. 1930.

Colonies on Czapek's solution agar growing rather restrictedly, about 2.0 to 2.5 cm. in 8 to 10 days at room temperature, radially furrowed, consisting of a comparatively thick felt 1.0 to 1.5 mm. deep (fig. 54A and D), with basal portion close-textured and fairly tough, with surface loose-textured, strictly velvety and heavy-sporing in some strains, in others light sporing and almost floccose but presenting a velvety appearance, or showing both in the same culture, with growing margin 1 to 2 mm. wide, pale yellow to rich orange in color, conidial areas developing in localized central to sub-central patches against a background of yellow to orange or orange-red vegetative mycelium (appearing studded with orange to orange-red granules when viewed under low magnification) in some strains, in others heavily sporing throughout with the massed conidial structures characterizing the colony, in blue-green shades near greenish glaucous blue to deep bluish gray-green (Ridgway, Pl. XLII); exudate limited to abundant, yellow to pale orange; odor not pronounced, suggesting mushrooms; reverse in bright orange-red shades near flame scarlet or mars orange to burnt sienna (R., Pl. II); conidiophores abundantly produced in some strains, sparingly in others, arising mostly from the substratum (fig. 54E) but sometimes from aerial hyphae, usually unbranched, varying in length from comparatively short up to 300 to 400μ by 2.0 to 2.5μ, apparently smooth-walled in some strains, granular in others, or showing both conditions in the same strain, walls sometimes studded with orange colored crystals when viewed dry, apices slightly enlarged or in some strains definitely vesicular up to 5.0 or 5.5μ; penicilli strictly monoverticillate consisting of compact terminal clusters of sterigmata, usually 6 to 10 or 12 in the verticil (fig. 54F), in some strains more, mostly 8 to 10μ by 2.0μ with apices parallel or divergent, bearing chains of conidia up to 100μ long, loosely parallel but not producing definite columns; conidia globose to subglobose, about 2.0 to 2.5μ in diameter with walls appearing finely roughened.

Colonies on steep agar growing more rapidly than on Czapek, up to 4.5 to 5.0 cm. in 10 to 12 days, radially furrowed (fig. 54B), texture as described above, with margin usually broad, yellow to orange-red in color,

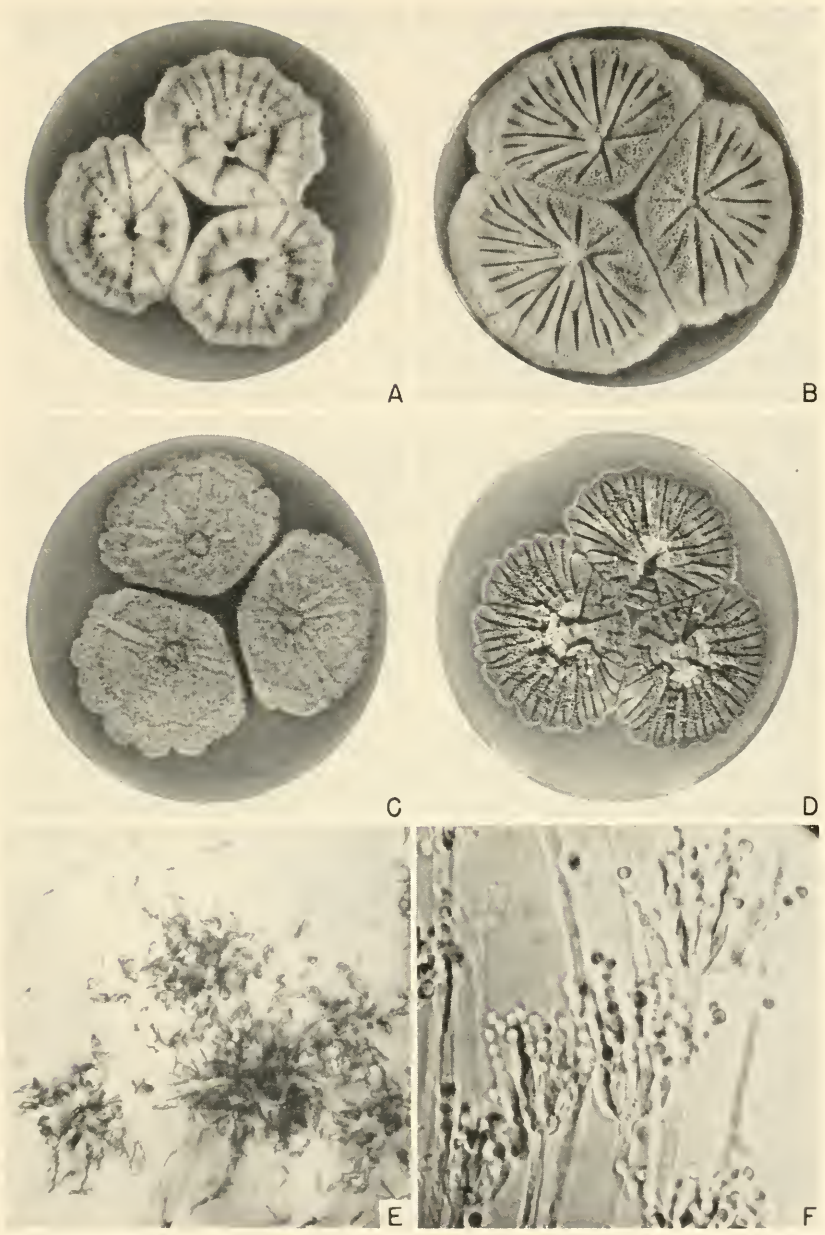


FIG. 54. *Penicillium multicolor* G.-M. and P. *A*, *B*, and *C*, Two-week-old colonies of strain NRRL 2058 on Czapek, steep, and malt agars, respectively; note heavy sporulation on malt. *D*, Colony of a closer textured, strictly velvety strain, NRRL 764, on Czapek agar. *E*, Low-power view of small secondary colonies showing divergent character of conidial chains, × 40. *F*, Detail of penicilli, × 900.

heavier sporing but in the same tints as on Czapek; exudate limited; odor not pronounced; penicilli as described above but with conidial chains longer, often exceeding 100μ.

Colonies on malt agar 3.0 to 4.0 cm. in 10 days, plane, appearing velvety commonly tufted in central colony areas (fig. 54C), in mixed red (from heavily encrusted vegetative hyphae) and blue-green (from conidial structures) shades, with the former predominating in some strains, the latter in others; exudate limited; odor not pronounced; reverse in bright orange-red shades near grenadine red or flame scarlet (R., Pl. II); conidiophores arising almost entirely from the substratum, bearing penicilli as described above but with conidial chains up to 150μ in length.

Species description centered upon NRRL 2058 received in May 1946, from Professor Weston, Harvard University, as a strain isolated from exposed textiles in Florida. Represented also by NRRL 2059 received in April 1944, from Laura A. Kolk, Brooklyn College, Brooklyn, New York, as a highly pigmented culture from a dilution plate of a water sample taken from a small pond. Also represented by NRRL 2060, received in May 1945 from Dr. Lawrence White, Philadelphia Quartermaster Depot, as a strain isolated in Florida from exposed cellulose-nitrate covered cellophane. When first received, this latter strain was diagnosed as *Penicillium implicatum* Biourge var. *aurco-marginatum* Thom. More careful examination of the strain indicates its proper placement to be with *P. multicolor* G.-M. and P.

Penicillium multicolor was isolated originally from Russian soil and was successfully cultivated upon a variety of substrata including potato, carrot, and beet. It did not coagulate milk, thrived in media containing 2 to 3 percent lactic acid, but grew poorly in alkaline media. It was characterized particularly by its pigmentation which varied with the substratum and ranged from yellow-orange to dark red, with pigment "grains" often appearing in the large hyphae. The penicilli were monoverticillate and usually unbranched.

Attempts to obtain the type culture failed. An organism bearing this name received from the authors was found to be replaced by another mold, or to have lost the characteristic features which distinguished it when first isolated. A form believed to approximate the type was subsequently sent to Thom by Professor Waksman as an isolate from New Jersey soil, but this was quickly lost from the collection. Another strain discussed by Thom in his Monograph (1930, p. 213) and in the laboratory was referred to as the "paint" organism, but under continued artificial cultivation lost its pigment producing power. Other strains suggestive of the *Penicillium multicolor* description were isolated from American sources but failed to survive for long periods in culture. Cultures of this type are apparently

not especially common in nature, but they have been encountered from time to time among soil isolates in this laboratory and have appeared among the strains isolated from deteriorating fabrics and other military equipment exposed in tropical and subtropical areas.

While we cannot assume with certainty that the highly colorful strains we assign to *Penicillium multicolor* G.-M. and P. duplicate in all details the strain originally examined by the authors of this species, there is considerable reason for believing that they must have based their species upon a monoverticillate form similar to those considered above.

Penicillium implicatum Biourge var. *aureo-marginatum* Thom (The Penicillia, pp. 211–212. 1930) created to include highly colored strains characterized by yellow-orange colony margins and yellow to reddish in reverse, is believed to represent *P. multicolor* G.-M. and P. Strains with conspicuously yellowed colony margins suggesting *P. implicatum*, but growing somewhat more rapidly and generally producing conidial areas in lighter blue-green shades, are occasionally encountered. Such a culture is contained in our Collection as NRRL 764. While we now regard it as a variant of *P. multicolor* it complies quite satisfactorily with Thom's diagnosis of *P. implicatum* var. *aureo-marginatum* as published in 1930.

Penicillium implicatum Biourge, in Monograph, La Cellule **33:** fasc. 1, pp. 278–280; Col. Pl. IX and Pl. XIV, fig. 82. 1923. Thom, The Penicillia, pp. 210–211. 1930.

Colonies on Czapek's solution agar (Col. Pl. IV) growing restrictedly, 1.5 to 2.0 cm. diameter in two weeks at room temperature, 200 to 300μ or more deep, with growing margin thin, narrow, and white (fig. 55A), often growing irregularly, gradually spreading to several centimeters with or without traces of zonation after several weeks, close-textured, tough, velvety or nearly so, very heavy sporing, umbonate, piled in center, showing some tendency to form crusts of conidia in age, nickel green to dark porcelain green (Ridgway, Pl. XXXIII) or dark Russian green (Pl. XLII); odor indistinct, weak or lacking; exudate lacking or limited, in small droplets, colorless, yellowish or in red-brown shades; reverse and agar yellow to orange to deep red-brown or maroon or occasionally purplish shades; conidiophores short, mostly under 100μ long by 2.0 to 2.5μ in diameter, arising generally from the substratum in a dense stand (fig. 55E) or occasionally borne as branches from trailing hyphae, smooth or nearly so; penicilli usually strictly monoverticillate but with an occasional branch which bears a verticil of sterigmata but retains its monoverticillate character, bearing conidial chains in loose columns up to 200μ or more in length; sterigmata closely packed, mostly 8 to 12 in the verticil, ranging from 9 to 12μ by 2.0 to 2.5μ (fig. 55F); conidia elliptical, 2.5 to 3.0μ by 2.0 to 2.5μ, many subglobose, 2.5 to 3.0μ, occasionally larger up to 4.5 to 5.0μ, heavy-walled, smooth or delicately roughened, dark green in mass.

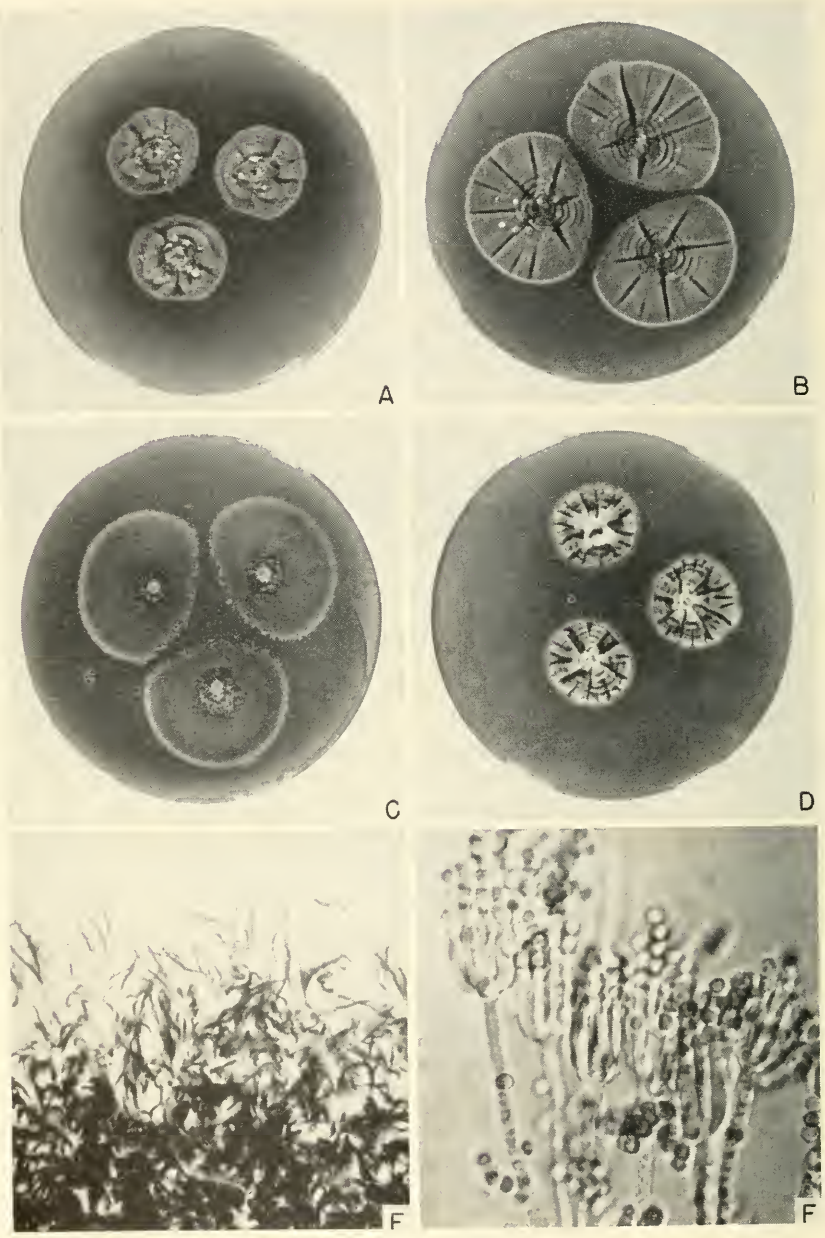


FIG. 55. *Penicillium implicatum* Biourge, NRRL 2054, and *P. sublateritium* Biourge, NRRL 2071. *A–C*, Two-week-old colonies of *P. implicatum* on Czapek, steep, and malt agars. *E*, Low-power view of the colony margin in the same strain, × 40. *F*, Detail of penicilli in same, × 900. *D*, *P. sublateritium* on Czapek agar, 2 weeks.

PLATE IV

TOP: Penicillium implicatum Biourge, NRRL 2054, on Czapek's solution agar, 12 days. *CENTER: Penicillium chermisinum* Biourge, NRRL 2049, on malt agar, 10 days. *BOTTOM: Penicillium vinaceum* Gilman and Abbott, NRRL 739, on Czapek's solution agar, 12 days. (Color photographs by Haines, Northern Regional Research Laboratory. Reproduced through co-operation of Chas. Pfizer & Co., Inc.)

Colonies on steep agar growing more rapidly, attaining a diameter of 3.0 to 4.0 cm. in two weeks at room temperature, radiately wrinkled (fig. 55B), particularly in central areas with marginal zones 1.0 to 1.5 cm. almost plane, somewhat zonate at center, very heavily sporing, in bluish gray-green shades to dark bluish gray-green (R., Pl. XLII) in some strains to gray-green approximating storm gray to castor gray (R., Pl. LII) in others; colony texture as on Czapek; penicilli as described above but producing columns of conidia up to 200μ or more in length, often producing definite crusts.

Colonies on malt extract agar 2.5 to 3.0 cm. in two weeks, plane (fig. 55C), often somewhat zonate in central areas, colony colors as described on Czapek; reverse in lighter colors, never reaching the deep red-brown or maroon shades described above; penicilli as described on Czapek, bearing chains of conidia in loose columns, 200μ or more in length, forming definite crusts in old cultures.

Species description centered upon NRRL Nos. 2054, 753, 743, and numerous other strains possessing essentially the same cultural and morphological characteristics. The species as described is drawn in broad enough terms to include a group of strains differing somewhat in particular characteristics, but showing sufficient similarity in general appearance and growth habits to be considered together. These forms are fairly common in soil and characteristically appear in soil dilution plates as restricted, heavily sporing, dark blue-green colonies with reverse in orange-brown to maroon shades. They occur frequently on fabrics and military equipment undergoing slow microbial attack. They are world-wide in distribution.

Typical strains of *Penicillium implicatum* upon all substrata show conidial areas in deep blue-green shades, with the blue element pronounced or even dominant. However, occasional strains, otherwise typical, develop conidial areas in yellow-green rather than blue-green shades. Recognition of a variety covering these forms is not considered advisable since the color change from strain to strain is progressive rather than abrupt and no satisfactory line of separation can be drawn. It is sufficient if the worker recognizes the presence of such variation.

Penicillium sublateritium Biourge, in Monograph, La Cellule **33:** fasc. 1, pp. 315–317; Col. Pl. X and Pl. XVI, fig. 92. 1923. Thom, The Penicillia, p. 222. 1930.

Colonies upon Czapek's solution agar restricted in growth, 1 to 2 cm. in diameter in 10 to 12 days at room temperature, appearing velvety with a white margin less than 1 mm. wide, rather deeply radiately wrinkled or furrowed, buckled in center (fig. 55D), faintly zonate, mycelium con-

sisting of slender hyphae developing a close-textured felt (aerial and submerged) about 400 to 500μ deep, firm but splitting rather easily, sporulating abundantly in gray-green shades from celandine green to puritan gray or court gray (Ridgway, Pl.XLVII); odor none; exudate not seen; reverse in shades of pale to dark orange-red approaching brick red (R., Pl. XIII); conidiophores mostly less than 100μ by about 2μ, occasionally longer, with walls smooth or slightly granular; penicilli strictly monoverticillate, consisting of small verticils of 5 to 8 or 10 parallel sterigmata, bearing spores in chains up to 100μ in length, becoming tangled in age; sterigmata mostly 10 to 12μ by 2.0 to 2.5μ, occasionally 15μ in length, commonly showing one or more under-developed cells in the verticil, tapering to rather broad conidium-producing tubes; conidia at first long, obpyriform to apiculate, often continuing so, more commonly becoming elliptical, 4.0 to 5.0μ by about 3.0μ, with walls smooth or finely granular.

Colonies on steep agar up to 3 cm. in diameter after 10 to 12 days at room temperature, velvety and wrinkled as on Czapek, azonate, reverse in darker shades of orange-yellow near vinaceous fawn (R., Pl. XL); penicilli as described above.

Colonies on malt agar 2 to 3 cm. in diameter in 10 to 12 days, looser textured and showing some trailing hyphae, less strongly wrinkled, more heavily sporing throughout; no odor; no exudate; reverse in golden brown shades; penicilli as described above but with sterigmata sometimes appearing irregular and with spore-bearing tubes longer, conidia usually long pyriform.

Species description centered upon a culture received in July 1946, from the Centraalbureau as a culture from Biourge bearing this name, presumably type, obtained by them in 1929. This culture is now maintained in our collection as NRRL 2071. Occasional strains produce colonies in darker yellow-green colors with reverse less strongly pigmented. NRRL 2072, received from Professor Weston as an isolate from deteriorating military equipment, Barro Colorado Island, Panama Canal Zone, is representative of these forms.

Biourge's species is recognized since his culture seems to represent, fairly well, a group of strains having the general cultural characteristics of the *Penicillium implicatum* series but producing large elliptical to obovate or pyriform spores. Proper placement of the species can only be guessed from Biourge's original description and figures. Thom in 1930 regarded it as no more than "a variety of the *P. frequentans* series of organisms". If the culture in our possession is authentic, this earlier assignment is regarded as untenable, since the culture in question differs markedly from *P. frequentans* in rate and pattern of growth, in size, and structure of the penicillus, and particularly in the dimensions and shape of the conidia. Conidial areas usually run toward yellow or gray-green rather

than the deep blue-greens of typical *P. implicatum*, and colonies in reverse are less deeply colored. Nevertheless, in rate of growth and in the type of colonies developed, the species appears to be closer to *P. implicatum* than any other well-recognized form.

Occurrence and Significance

Members of the *Penicillium implicatum* series are not infrequently isolated from soil, and have been encountered rather commonly among the Penicillia isolated from fabrics and other types of military equipment undergoing deterioration in the field. Their significance under such conditions is largely a matter of conjecture. No biochemical studies are known to have been based upon either of the three species which comprise the series.

Penicillium decumbens Series

Outstanding Characters

Colonies slow-growing usually restricted, superficially appearing velvety or lightly floccose, consisting of networks of trailing and interwoven vegetative hyphae, ranging from comparatively loose-textured in some species to dense, tough mycelial felts in others.

Penicilli strictly monoverticillate and consistently small, typically borne on short, lateral branches (conidiophores) from trailing, looping or interwoven aerial hyphae, seldom arising directly from the substratum.

Conidia small, usually somewhat elliptical, about 2.0 to 3.0μ in long axis with walls smooth in most forms, delicately roughened in others.

Vegetative mycelium delicate, thin-walled.

Series Key

2. Colonies appearing velvety or with surface lightly floccose; conidiophores borne primarily as short branches from loosely trailing or compacted vegetative hyphae..... *P. decumbens* series
   a. Colonies loose-textured, with margin usually thin and generally consisting of a loose network of interlacing hyphae bearing short conidiophores.
      1′. Conidial areas in light gray-green shades with reverse uncolored or in yellow drab shades on Czapek agar but becoming cherry red on malt and wort agars..... *P. chermesinum* Biourge
      2′. Conidial areas in dull blue-green shades with reverse usually uncolored on all media..... *P. decumbens* Thom
   b. Colonies close-textured, tough, almost leathery, restricted, with margin compact but showing occasional stolon-like hyphae.
      1′. Vegetative mycelium yellow, generally characterizing the colony even in age, sporulating lightly on Czapek agar..... *P. citreo-viride* Biourge
      2′. Vegetative mycelium white, often characterizing the colony when young, but developing blue-green conidial areas in one to two weeks, reverse uncolored or in light vinaceous gray shades..... *P. fellutanum* Biourge
      3′. Vegetative mycelium white to pale vinaceous, sparsely sporulating, reverse bright orange-red to maroon..... *P. roseo-purpureum* Dierckx

Members of this series appear to be fairly abundant in nature and are world-wide in distribution. They regularly occur in soil dilution plates, but due to their restricted growth may be easily overlooked, or become quickly overrun by more vigorously growing species. They are apparently better adapted to growth in the presence of limited nutrients, or under alternate wet and dry conditions, than many Penicillia, for they occur with unusual frequncy among the molds isolated from military equipment undergoing deterioration under field conditions.

The *Penicillium decumbens* series, as it is considered here, includes a range of forms rather divergent in some respects but uniformly characterized by the production of small monoverticillate penicilli borne on short branches (or conidiophores) arising from trailing or interlacing hyphae (fig. 56) Upon the basis of general colony texture, the series can be subdivided into two fairly well defined sub-series.

The first of these, typified by *Penicillium decumbens* Thom, is characterized by comparatively slow growing but loose-textured colonies in which the trailing, penicilli-bearing hyphae are loosely interwoven and retain considerable individuality (see fig. 57C). In addition to *P. decumbens*, this sub-series includes *P. chermesinum* Biourge, which is characterized by its more rapid growth and its development of bright red colors in colony reverse on malt and wort agars.

The second sub-series, typified by *Penicillium fellutanum* Biourge, is characterized by the development of restricted, tough, almost leathery basal felts, from the surface and margins of which arise trailing aerial hyphae bearing small penicilli on short conidiophores in the manner typical of the series. Also, included here are *P. citreo-viride* Biourge, a very slow-growing, tardily sporulating form which produces small, raised colonies with surface and reverse bright yellow on Czapek's solution agar; and *P. rosco-purpureum* Dierckx, equally slow-growing, tardily sporulating and almost floccose, producing abundant orange-red to vinaceous pigment in the exudate and the colony reverse.

Penicillium chermesinum Biourge, in Monograph, La Cellule **33:** fasc. 1, pp. 284–285; Col. Pl. X and Pl. XVI, fig. 95. 1923. Also Thom, The Penicillia, pp. 192–193. 1930.

Colonies on Czapek's solution agar growing fairly rapidly, attaining a diameter of 4.0 to 5.0 cm. in 2 weeks at room temperature, broadly zonate, radiately wrinkled and buckled, surface tufted, granular (fig. 57A), consisting of a woven mass of hyphae and ropes of hyphae bearing conidiophores as short branches, rather light sporing, fruiting areas in greenish gray shades near mineral gray (Ridgway, Pl. XLVII), unevenly distributed, generally denser in central areas, conspicuous zones sometimes evi

dent in marginal areas; odor faint, suggesting wood smoke; exudate limited, occurring either as numerous small droplets or few large ones,

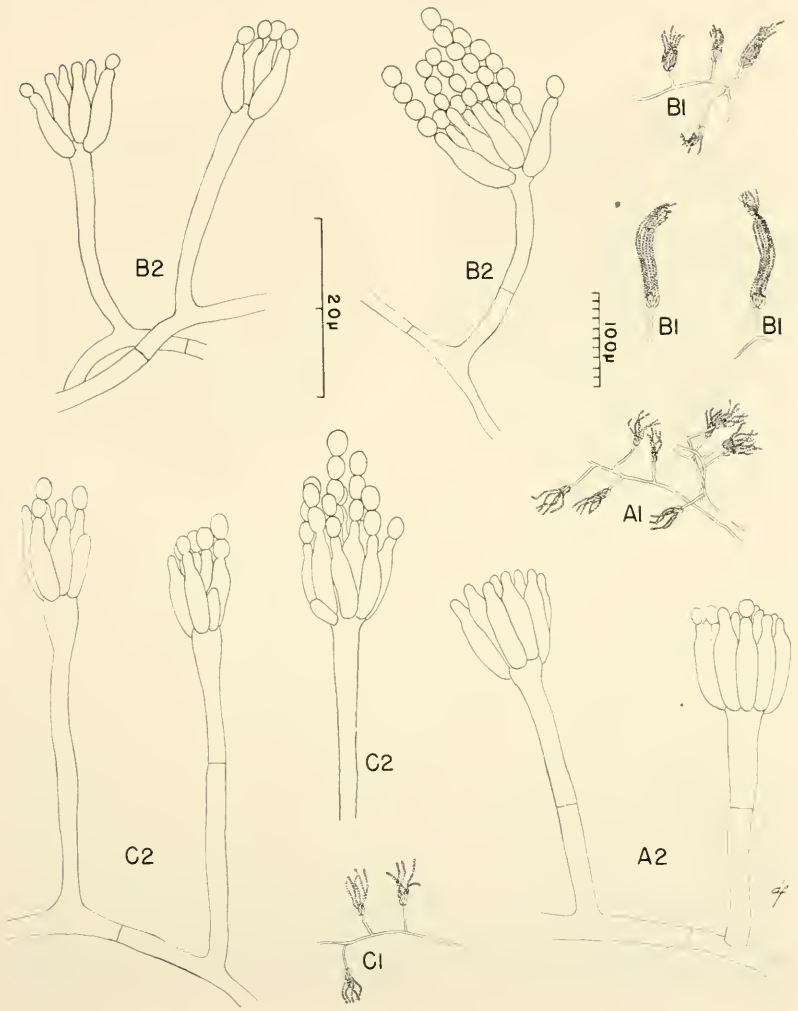


FIG. 56. *Penicillium decumbens* series. *A*, *P. chermesinum* Biourge. *B*, *P. decumbens* Thom. *C*, *P. fellutanum* Biourge. A_1, B_1, and C_1, Habit sketches of representative penicilli. A_2, B_2, and C_2, Detailed drawings of penicilli. This series is characterized particularly by its short conidiophores which arise almost exclusively from aerial hyphae.

clear; reverse in light yellow to flesh or clay colors; conidiophores borne entirely as short branches from loosely interwoven and trailing hyphae (fig. 57C), smooth-walled, mostly 20 to 40μ by 2.0 to 2.5μ, some up to 50μ

long, apices swollen to form definite vesicles 4.0 to 4.5μ in diameter; penicilli strictly monoverticillate with no branched structures observed, bearing loose to fairly compact columns up to 100μ in length; sterigmata crowded, often incurved, usually 10 to 15 in the verticil, about 6 to 8μ

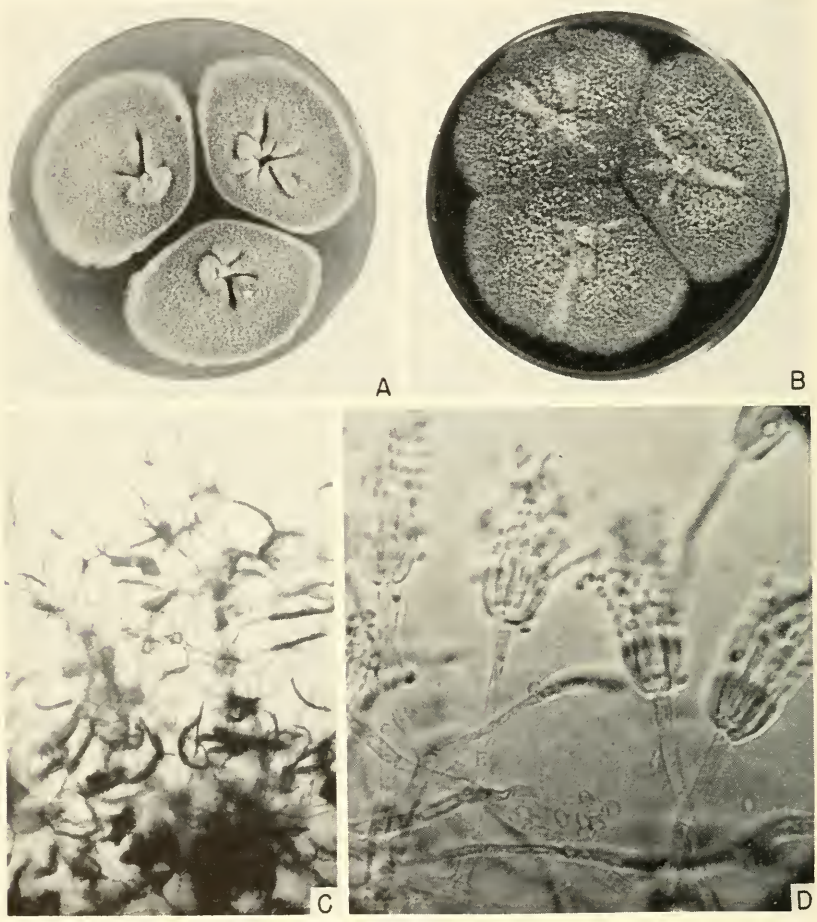


FIG. 57. *Penicillium chermesinum* Biourge, NRRL 2048. *A* and *B*, Two-week-old colonies on Czapek and malt agars. *C*, Low-power view of colony margin showing conidiophores as short branches from interlacing aerial hyphae, × 100. *D*, Detail of penicilli; showing also the origin of conidiophores, × 900.

by 2.0 to 2.5μ (fig. 57D); conidia elliptical, smooth, 2.0 to 2.5 by 1.5 to 2.0μ, appearing faintly green in mass.

Colonies on steep agar attaining a diameter of 5.5 to 6.0 cm. in 2 weeks, with texture as described on Czapek except even more granular and some-

what looser and deeper; consistently heavily sporing, in some strains abundantly; exudate clear, somewhat more abundant than on Czapek; reverse uncolored to very light cream or tan shades; penicilli as described above, but sterigmata more numerous in the verticil, usually 15 to 20 and somewhat longer, measuring 8 to 10μ.

Colonies on malt extract agar (Col. Pl. IV) growing somewhat less rapidly than on steep agar, 5.0 to 5.5 cm. in diameter, generally plane and usually showing a thin overgrowth of white to light flesh-colored aerial mycelium (fig. 57B), sporulating to the colony edge; in some strains showing a marked tendency to develop sectors; exudate entirely lacking; reverse and agar in deep blood to wine red shades, this color in reverse on malt agar being one of the main distinguishing characteristics of the species; penicilli as described above, with sterigmata numerous in the verticil and strongly incurved.

Species description centered upon NRRL 2048, NRRL 2049, and many additional strains showing similar cultural and morphological characteristics. The species appears to be fairly abundant in nature and has been repeatedly encountered among the molds isolated from deteriorating fabrics and other material. It should probably be regarded as essentially a soil organism since most of the strains examined have been obtained from organic substrata subject to contact with the soil or to dust contamination.

The forms under consideration are believed to approximate that originally described by Biourge under this name, although no material which can now be regarded as typical, is available to definitely establish this fact. NRRL 735 (Thom's No. 4733.29) received from Biourge in 1924 as type is not acceptable for the species since it produces large, globose conidia, colonies almost sterile, and reverse not strongly colored on malt agar. *Penicillium chermesinum* Biourge was reported to be a monoverticillate form with conidiophores arising from creeping hyphae, conidial areas green to gray olive in color, with conidia small, elliptical and smooth-walled, and with colony reverse on wort, orange-yellow to purplish red to dark reddish brown. The strains under observation seem to conform with this diagnosis better than that of any other described species.

Penicillium decumbens Thom, in U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, p. 71, fig. 28. 1910. Also Thom, The Penicillia, pp. 197–198, fig. 24. 1930.

Colonies on Czapek's solution agar slowly spreading, attaining a diameter of 2.0 to 3.0 cm. in 12 to 14 days at room temperature, almost velvety in some strains, in others showing a tendency to develop white mycelial overgrowths in central areas (fig. 58A), in still others almost floccose and

fairly deep up to 1 to 2 mm. but all characterized by loosely interwoven and trailing hyphae bearing short conidiophores, sporulating over the whole colony surface, marginal growth in some strains very thin, largely submerged in zones from 1 to 3 mm. wide, colored in grayish yellow-green shades near gnaphalium to tea green (Ridgway, Pl. XLVII), in older

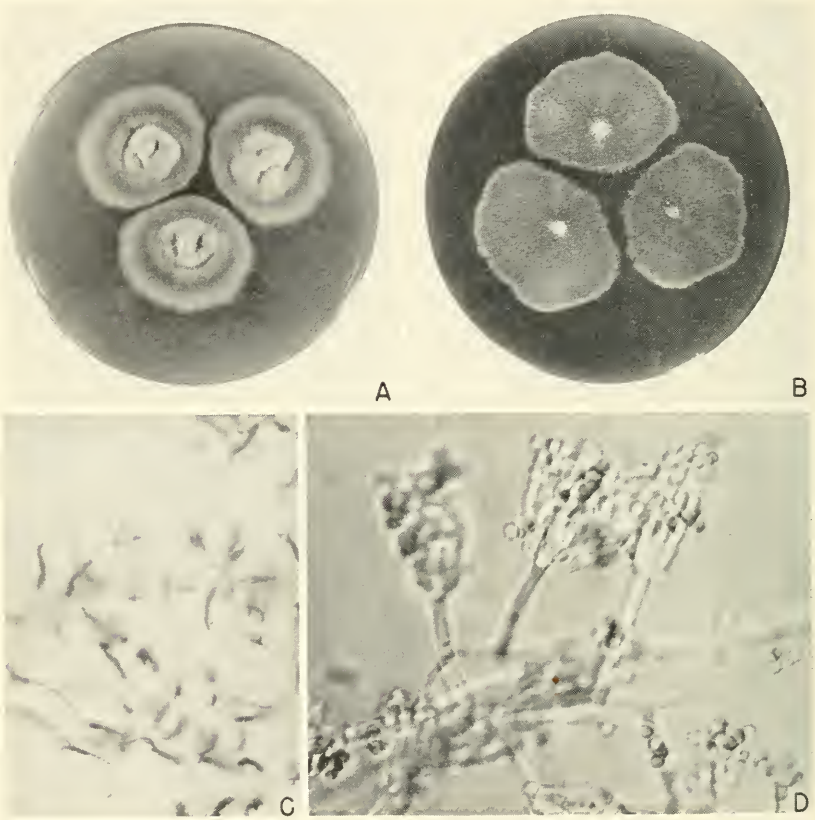


FIG. 58. *Penicillium decumbens* Thom, NRRL 742. *A* and *B*, Two-week-old colonies on Czapek and malt agars. *C*, Low-power view of colony margin showing conidial structures borne as short branches from aerial and looping hyphae, × 100. *D*, Detail of structure and origin of penicilli, × 900.

colonies developing surface tufts of sterile secondary mycelium; exudate lacking or inconspicuous; odor distinctive, fragrant, suggesting soap perfumes; reverse colorless or with a slight greenish cast; conidiophores 50 to 100μ by 2.0 to 2.5μ, with apices slightly enlarged, smooth or finely roughened, borne at successive nodes upon trailing hyphae (fig. 58C) which in marginal areas of many strains grow stolon-like along the substratum;

penicilli almost entirely monoverticillate and only occasionally showing a branch, producing loose columns of conidia up to 100μ in length; sterigmata mostly in compact clusters up to 12 or 15 in number, 7 to 9μ by 2.0 to 2.5μ (fig. 58D), sometimes borne at two immediately adjacent levels; conidia elliptical to subglobose 2.0 to 2.5μ in long axis, occasionally up to 3.0μ, smooth, appearing slightly green under the microscope.

Colonies on steep agar 3.0 to 4.0 cm. in 2 weeks, usually deeper than on Czapek and showing a more definite margin without submerged zone, central colony areas in dull green shades becoming drab in age; reverse almost colorless to slight yellow or orange shades; penicilli more abundantly produced and often somewhat larger than on Czapek.

Colonies on malt extract agar growing more rapidly, up to 4.0 to 6.0 cm. in 2 weeks, plane (fig. 58B) with coloration as described on Czapek but fading in age to gray-brown shades, very heavily sporing; penicilli as described above but producing loose columns of conidia up to 250μ long.

Species description centered upon NRRL 742 received in 1933 from Professor C. D. Sherbakoff, University of Tennessee, Knoxville, and several other strains, primarily from soil and deteriorating military equipment, that present the same general morphology. The species appears to be fairly common and is probably world-wide in distribution, since strains from South Africa, Liberia, Panama, the South Pacific Area, and various stations in the United States have been examined. It is characterized primarily by its comparatively thin, loose network of trailing hyphae bearing numerous short-stemmed monoverticillate conidial structures, its coloration, and its distinctly fragrant odor.

Thom's original description was based upon a strain contributed in 1905 by Professor P. H. Rolfs from Miami, Florida. This was subsequently lost from his collection, but had been sent to Kräl in Prague. This strain was subsequently returned to us by Biourge in 1924 and is now maintained in the Collection as NRRL 741. In our current comparative study it differs from the species as described only in producing colonies of somewhat closer texture that are definitely lighter sporing. The authenticity of the type is not questioned although it has become somewhat altered during forty years of laboratory cultivation. The present species description has been broadened somewhat beyond Thom's original description (1910) to cover a clearly related group of molds with fairly uniform morphology.

A culture received from the Centraalbureau under this name, now maintained as NRRL 2044, represents the species satisfactorily but tends to produce colonies somewhat deeper and of looser texture than NRRL 742 and similar strains. The details of the penicillus, coloration, and the production of the characteristic fragrant odor are the same. A strain

received as *Penicillium dierckxii* Biourge duplicates the one received as *P. decumbens* and should properly be regarded as belonging to the latter species.

Penicillium fellutanum Biourge, in Monograph, La Cellule **33:** fasc. 1, pp. 262–264, Col. Pl. XIII and Pl. XXIII, fig. 133. 1923. See also Thom, The Penicillia, pp. 198–199, fig. 25. 1930.

Colonies on Czapek's solution agar restricted in growth, about 2.0 to 2.5 cm. in diameter in 12 to 14 days at room temperature, consisting of a tough, closely woven felt of fine hyphae, 100 to 200μ in depth (fig. 59A), with margin thin and often extending beyond the colony margin as a narrow zone of predominantly submerged growth, composed of funiculose stolon-like hyphae, becoming deeper and almost umbonate at colony center, radiately wrinkled, narrowly zonate, in some strains light sporing, with central colony area commonly remaining white, developing marginal conidial areas in bluish green shades near gnaphalium green to sage green (Ridgway, Pl. XLVII), becoming slate-olive in age; exudate lacking or limited in amount, when present produced as small droplets, clear or very light amber; odor distinct, rather pleasant; reverse cream to flesh colored or in light vinaceous gray shades, in some strains showing some green; conidiophores usually 50 to 100μ in length by 2.0 to 2.5μ in diameter, smooth-walled, arising from a closely woven felt, or from trailing or prostrate creeping hyphae, generally enlarging upward to form more or less well-defined vesicles with upper surface often definitely flattened and from 4.0 to 5.0μ in diameter; penicilli usually strictly monoverticillate but occasionally showing a branch which retains its monoverticillate structure, conidia borne in poorly defined columns up to 100μ in length; sterigmata in compact verticils up to 8 to 12 in number, usually 6 to 8μ by 1.5 to 2.2μ (fig. 59D); conidia elliptical to subglobose, mostly about 2.5 to 3.0μ in long axis, fairly heavy-walled and smooth or finely roughened, dull green in mass.

Colonies on steep agar differ little from those on Czapek but are somewhat faster growing, 3.0 to 3.5 cm. in diameter in 2 weeks, generally deeper, more heavily sporing (fig. 59B), mostly in dark green shades, and with masses of conidia somewhat heavier; conidiophores up to 300μ long in some strains, commonly arising from the substratum; penicilli structurally as on Czapek except sterigmata are more numerous, often in clusters of 12 to 15.

Colonies on malt extract agar restricted, about 1.5 to 2.0 cm. in diameter, plane except slightly umbonate at center (fig. 59C), generally heavy sporing; conidiophores and penicilli as on Czapek but bearing loose columns of spores up to 200μ in length on conidiophores up to 150 to 200μ.

Species description based upon Thom's notes made on Biourge's type (Thom's No. 4733.58—now lost from this collection) prior to 1928, and upon comparative observations made during the current study on a number of strains regarded as representative of the species. Among such cultures may be listed NRRL 746, received in 1935 from Dr. Oscar W. Richards, then at Yale University; NRRL 1196 received in 1940 from Dr. G. A.

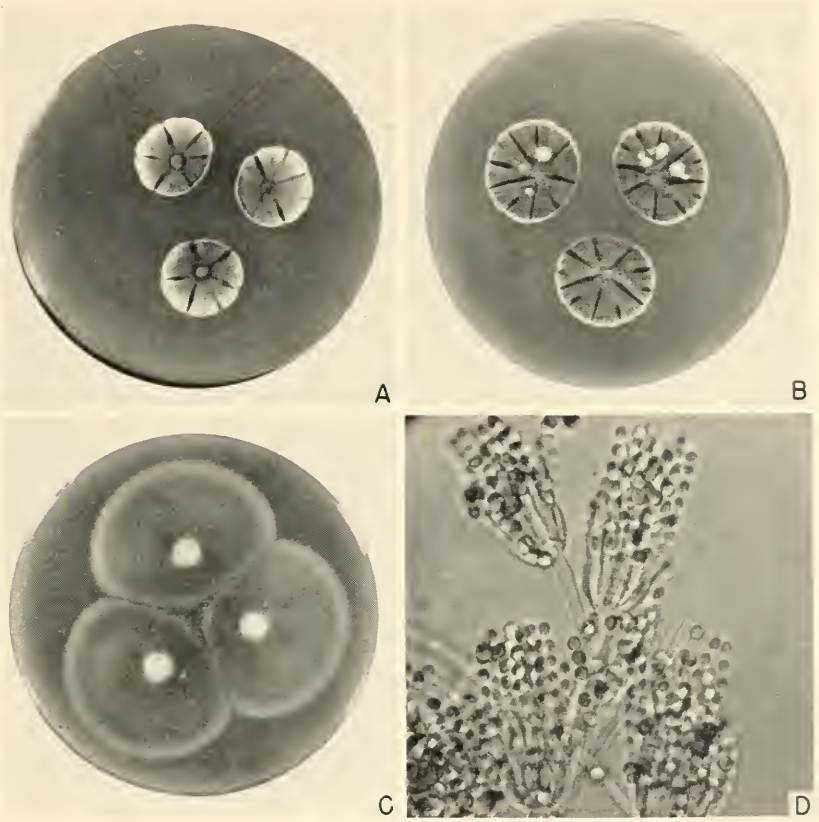


FIG. 59. *Penicillium fellutanum* Biourge, NRRL 746. *A*, *B*, and *C*, Two-week-old colonies on Czapek, steep, and malt agars. *D*, Detail of penicilli, × 900.

Ledingham, Ottawa, Canada; and numerous strains isolated by various investigators from deteriorating military equipment in tropical and subtropical areas and submitted to us for identification.

Strains included within the species have the same morphology of conidial structures, but show considerable individuality in rates of growth and in cultural aspects—such as the compactness of superficial growth, color, and in the specific character of the colony margin.

NRRL 2045, received in May 1946 from Professor W. H. Weston as an isolate from deteriorating tentage in the Canal Zone, represents something of an extreme in producing very restricted and exceedingly close-textured colonies that are strongly raised and frequently split open in central areas; penicilli are typically smaller and are borne upon very short conidiophores arising from closely felted hyphae. This culture may be regarded as approximating the one cited by Thom in his Monograph (1930, p. 199) as strain number 4876.24, received originally from Westerdijk.

NRRL 749 is representative of variation in another direction. Colonies on Czapek are larger, up to 3.0 cm. in 2 weeks, comparatively thin, very strongly wrinkled, with central areas commonly depressed and with subcentral areas raised and often splitting from the extreme folding of the mycelium, more or less zonate, rather heavy sporing in dull yellow to gray-green shades, and with reverse yellow to drab but not in vinaceous or greenish shades; the penicilli are characteristic of the species in origin and in pattern.

NRRL 2068 is representative of a group of very slow-growing strains isolated from fabrics and other military equipment undergoing deterioration in tropical and subtropical areas. Colonies grow very restrictedly on all media, and on Czapek, commonly show no evident growth for several days after inoculation and reach a diameter of 1 cm. only after 10 to 14 days. Colonies are very close-textured, tough, with central areas uncolored or pinkish, with exudate clear to light amber, and showing limited conidial development only in submarginal areas. Colonies on malt agar are similarly restricted but heavier sporing and in somewhat lighter yellow-green shades than such typical strains as NRRL 746. The penicilli are typical of the species in origin and in pattern.

Three additional species described by Biourge are believed to represent little more than strain differences, hence to belong with his *Penicillium fellutanum*. The types upon which these species were based show limited strain individuality, but are not believed to show sufficient differences one from the other or from *P. fellutanum* to warrant their continued recognition.

Penicillium phaeo-janthinellum Biourge (Monograph, La Cellule **33**: fasc. 1, pp. 289–290; Col. Pl. VIII and Pl. XIII, fig. 77. 1923) as described and illustrated by him, seems to approximate *P. fellutanum*. No authentic material has been available for the present study, but Thom's notes made prior to 1930 on Biourge's type (Thom's No. 4733.96) indicate a culture of the type discussed above, which apparently differed from these only in being somewhat faster growing (4.0 cm. diam. in 2 weeks) and possibly looser in texture. A strain received from the Centraalbureau in July 1946, bearing this name, as an isolate from "Gambir" in 1927, shows limited strain individuality but lacks essential differences to separate it from *P. fellutanum* Biourge as the species is considered here.

Penicillium dierckxii Biourge (Monograph, La Cellule **33:** fasc. 1, pp. 313–315; Col. Pl. X and Pl. XVI, fig. 91. 1923) was described in terms approximating *P. fellutanum* of the same author, except for the development of reddish brown to dark blood red colors in reverse on wort gelatine. Thom's study of the type strain No. 4733.50 (now maintained as NRRL 755) in 1928 generally confirmed Biourge's description. Examination of NRRL 755 for the present study shows colonies restricted but less highly colored in reverse, conidiophores longer and commonly branched in the terminal area, and conidia averaging somewhat larger than reported by Thom (1930). There is some question, therefore, whether NRRL 755 adequately represents Biourge's organism. In the absence of any other strains which are clearly assignable to *P. dierckxii*, we believe that it can best be regarded as having represented a variant member of what we now consider *P. fellutanum* Biourge.

Penicillium cinerascens Biourge (Monograph, La Cellule **33:** fasc. 1, pp. 308–309; Col. Pl. IX and Pl. XIV, fig. 81. 1923) is believed to approximate *P. fellutanum* of the same author. Colonies were described as restricted with trailing or ascending hyphae, at first slightly bluish green, then gray-green to gray and at length reddish brown, reverse pale yellow, conidiophores smooth-walled and short, about 35,μ and borne upon ascending (aerial) hyphae; conidia were described as oblong to globose and rough echinulate when ripe. Only in the character of the conidia does the species differ substantially from *P. fellutanum*, and in Biourge's figures these are shown as oblong to elliptical and apparently smooth-walled. Thom failed to receive Biourge's number 50, the type strain, but did receive his number 90, labeled *P. cinerascens*. This latter culture is discussed by Thom in his Monograph (1930, p. 201) as number 4733.34 and agrees reasonably well with Biourge's observations except conidiophores were reported as substantially longer, and the conidia as elliptical to globose and (apparently) smooth-walled. This latter culture is now maintained in our collection as NRRL 748 and retains the characteristics reported by Thom. The strain, while culturally distinct, belongs in the series with *P. fellutanum* Biourge and is not believed to warrant recognition as a separate species.

Penicillium citreo-viride Biourge, in Monograph, La Cellule **33:** fasc. 1, p. 299; Col. Pl. IX and Pl. XV, fig. 88. 1923. Also Thom, The Penicillia, pp. 199–200. 1930.

Colonies on Czapek's solution agar growing restrictedly, attaining a diameter of 2.0 to 3.0 cm. in 12 to 14 days at room temperature, strongly wrinkled and buckled, with center umbonate in some colonies, depressed in others (fig. 60A), consisting of a tough mycelial felt 100 to 200μ or more deep but thinning to a fibrous margin, in most strains conspicuously yellow in color, near citrine to pinard yellow (Ridgway, Pl. IV), and showing very little conidial development up to 2 weeks or more, in other strains sporulating less tardily and becoming dull gray near mineral to court gray (R., Pl. XLVII) in about 10 to 14 days, with surface appearing velvety or very lightly floccose, vegetative hyphae delicate and yellow in color; exudate not produced in some strains, limited in others, in light citrine shades; odor slight, moldy; reverse and agar in bright yellow shades during the growing period, in some strains becoming darker in age; conidio-

phores arising mainly from trailing and branching hyphae, smooth-walled mostly 50 to 100μ by 1.6 to 2.2μ but sometimes arising from the substratum and longer, up to 150μ; penicilli mostly simple monoverticillate (fig. 60D), occasionally showing a prolongation of the main axis, or with 1 or 2 branches from lower nodes producing secondary verticils of sterigmata, bearing conidial chains up to 50μ or more in length, loosely parallel or

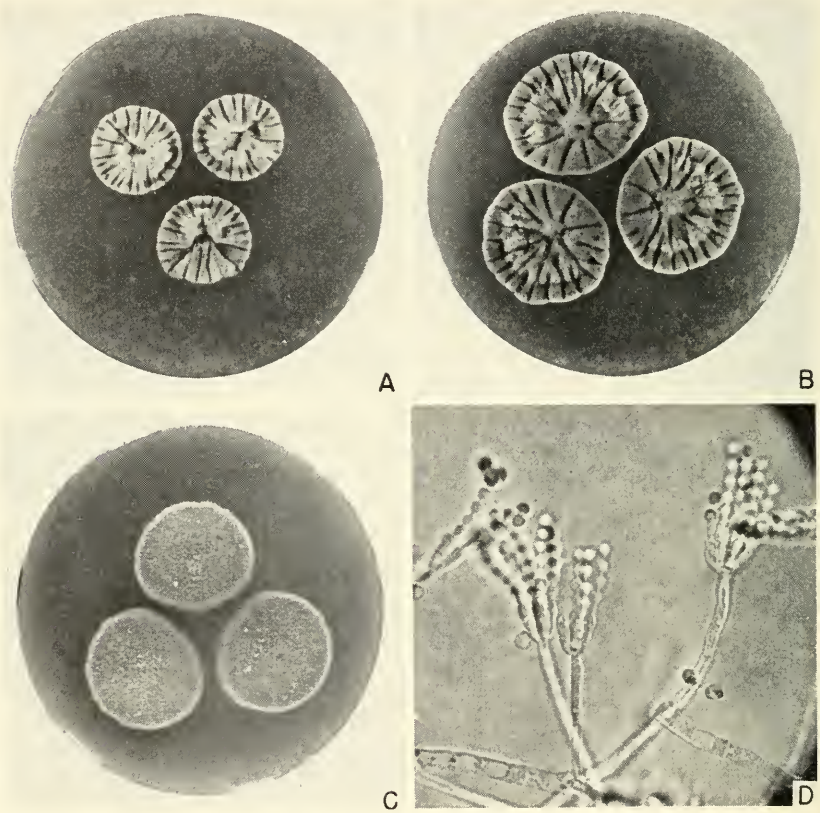


FIG. 60. *Penicillium eitreo-viride* Biourge, NRRL 2047. *A*, *B*, and *C*, Two-week-old colonies on Czapek, steep, and malt agars. *D*, Detail of small penicilli characteristic of species, × 900.

slightly diverging, not adherent into solid columns; sterigmata in compact clusters of 8 to 12, mostly 9 to 12μ by 2.2 to 2.8μ, with fairly long conidial tubes; conidia globose, 2.2 to 2.8μ, thin-walled, smooth or nearly so, adherent in chains with connectives evident.

Colonies on steep agar growing more rapidly, 3.0 to 4.0 cm. wide in 2 weeks, broadly and radiately furrowed (fig. 60B), velvety in appearance,

sporulating abundantly over the whole colony surface from a basal mycelial felt yellow in color and in texture as described above, conidial color as on Czapek but quickly changing to gray shades in central area and becoming mouse gray in age; exudate more abundant; reverse and agar in yellow shades, becoming orange-brown under central colony areas; penicilli as described above.

Colonies on malt extract agar spreading fairly broadly, 4.0 to 5.0 cm. in 2 weeks, plane, slightly zonate, or azonate (fig. 60C), heavily sporing throughout, color as in sporulating areas on Czapek; reverse in dull yellow-brown to red-brown shades; conidial structures as described above.

Species description based upon our observations of NRRL 1187, NRRL 2046, NRRL 2047, and other strains having similar morphology combined with Thom's original notes (see Monograph, 1930, p. 200) made from Biourge's type strain, now lost from our Collection. The species has appeared repeatedly among cultures isolated from deteriorating military equipment submitted to us for identification, and strains NRRL 2046 and 2047 are of this origin. The species should be regarded as a soil organism widely distributed in nature. It is apparently able to grow under conditions of limited moisture and nutrients that would exclude many faster growing species.

Representatives of this species, as examined by us, vary substantially in gross cultural appearance, in relative abundance of sporulation, and to a lesser degree in details of morphology. There is reason to believe that earlier workers may have based species description upon variants or strains now known to represent different aspects of the same species complex. Five such species are believed to represent *Penicillium citreo-viride* Biourge as this species is regarded here.

Penicillium citreo-nigrum Dierckx, (Soc. Scient. Bruxelles **25**: p. 86. 1901; also Biourge's Monograph, La Cellule **33**: fasc. 1, pp. 273–274, Col. Pl. IX and Pl. XV, fig. 87. 1923) as represented by NRRL 761 (Thom's No. 4733.35), received from Biourge under this name in 1924, duplicates *P. citreo-viride* except colonies are thinner and somewhat faster growing, margins tend to be thin and often more or less submerged in a zone 2 to 3 mm. wide; but the general colony texture and coloration, and the structure of the penicillus are as described above. A culture from the Centraalbureau under this name, originally from Biourge and presumably of the same origin, duplicates even more exactly the cultures here regarded as representing *P. citreo-viride*. In the absence of any substantial differences in the original descriptions of *P. citreo-viride* Biourge and *P. citreo-nigrum* Dierckx as reported by Biourge, we believe that the latter should properly be regarded as a synonym. Our description of *P. citreo-viride* Biourge is accordingly drawn in broad enough terms to include the two cultures in question.

Penicillium citreo-sulfuratum Biourge (Monograph, La Cellule **33**: fasc. 1, pp. 285–287, Col. Pl. IX, and Pl. XV, fig. 86. 1923) is believed to be synonymous with his

P. citreo-viride. Biourge's original description and figures point to the identity of the two forms within the limits of average strain variability. A culture from the Centraalbureau in 1946 under this name (as originally from Biourge), is not strictly monoverticillate and shows little or no yellow color in mycelium or colony reverse, the characters upon which the species was originally based. The strain in question approximates *P. jenseni* Zaleski in the Divaricata.

Penicillium subcinereum Westling (Arkiv för Botanik **11:** 137–139, fig. 80. 1911) was regarded by Biourge (Monogr., p. 273. 1923) as a synonym of *P. citreo-nigrum* Dierckx. Biourge apparently obtained a culture from Amsterdam (Westerdijk) as *P. subcinereum* and identified it with Dierckx's organism from unpublished notes and colored plates. Both species are here regarded as synonymous with *P. citreo-viride* Biourge.

Citromyces sormanii Carbone (Atti. Ist. Bot. dell Universita Pavia, Ser. II, **14:** 290–295, 321, Taf. XII, figs. 2, 3, 4. 1910) was isolated from Italian sausages and cultivated upon various media. Certain characters stand out in Carbone's Latin diagnosis: Colonies glaucous; sterile hyphae about 1μ diameter—hence a fine close felt; conidiophores simple or branched (in the figure borne as short branches of trailing hyphae), broadening to a clavate apex, 132μ long by 1.5μ in diameter, conidial mass forming a column; sterigmata 3 to 6 in the verticil, 7 by 2.5μ; conidia in long chains, green, smooth, 2μ in diameter. This species has not been identified since described, hence does not appear in any collection but probably was near *Penicillium citreo-viride* Biourge.

Penicillium necrosiferum Morotchkovsky (Bul. Sci. Rec. Biol. Univ. Kiev. **2:** 79, fig. 9. 1936) was described in terms which seem to relate it to *P. citreo-viride* Biourge. The type has not been seen. A translation of the latin diagnosis follows: Colonies at first white, at length yellowish, with water drops numerous, yellow, round, convex, radiately furrowed with margin somewhat elevated, snowy white lanose; reverse yellowish green; submerged hyphae, colorless, branched, septate, with cells 22 to 27 even to 48μ long by 4.0 to 4.5μ in diameter; conidiophores arising from aerial hyphae unbranched or branched with apices inflated, erect, smooth, 40 to 81μ by 2.5 to 3.0μ; sterigmata 4, 6, or 8μ by 2.7μ; conidia at first elliptical in chains, then globose, 2.0 to 2.5μ in diameter, slightly yellowish without connectives; no coremia; odor lacking.

Penicillium roseo-purpureum Dierckx, in Soc. Scientifique Bruxelles **25:** p. 86. 1901. Biourge, Monograph, La Cellule **33:** fasc. 1, pp. 317–319; Col. Pl. X, Pl. XVI., fig. 96. 1923; *ibid.* **36:** 482. 1925. Also Thom, The Penicillia, p. 181. 1930.

Colonies on Czapek's solution agar growing restrictedly, attaining a diameter of 1.5 to 2.0 cm. in 12 to 14 days in most strains, up to 2.5 to 3.0 cm. in others, raised in central areas, deeply wrinkled, in some strains in radial pattern only, in others showing concentric ridges and irregular folding in central area, margins abrupt, consisting of a tough, closely woven felt of fine hyphae, very light sporing, mostly grayish white to flesh colored or pale pink, becoming light grayish green near gnaphalium to pea green (Ridgway, Pl. XLVII) in marginal areas where conidium production is most abundant; exudate lacking or limited in some strains,

abundant in others, in pink to vinaceous shades; odor faint, indefinite; reverse in red-orange shades near congo pink or terra cotta (R., Pl. XXVIII) to Prussian red (R., Pl. XXVII) with agar similarly but less intensely colored; conidiophores arising mostly as short branches from trailing and interwoven aerial hyphae, less than 50μ in length by 1.5 to 2.0μ in diameter, occasionally from submerged hyphae, 50 to 100μ in length, very rarely branched, smooth-walled; penicilli monoverticillate, consisting of a terminal verticil of very few to 8 or 10 sterigmata bearing loosely parallel to tangled chains of conidia up to 100μ in length in heavier sporing strains; sterigmata about 6 to 7μ by 1.5 to 2.0μ; conidia globose or nearly so, about 2.0 to 2.2μ, rarely 2.5μ with walls delicately roughened.

Colonies on steep agar as above in pattern and texture but growing somewhat more rapidly, 3.0 to 3.5 cm. in 2 weeks, slightly heavier sporing, more frequently producing abundant vinaceous exudate and more deeply colored in reverse; conidial structures as described above.

Colonies on malt agar growing restrictedly as on Czapek but looser textured and heavier sporing, light gray-green; no exudate; odor lacking or indefinite; reverse in dull orange-brown to deep brown shades; penicilli as described above, borne on short branches from trailing or decumbent hyphae with conidia in loose columns.

Species description based upon NRRL 2064, received in August 1946, from the Centraalbureau as a culture bearing this name from Biourge in 1929, presumably type; also, NRRL 2065 isolated in January 1946, from a sample of soil from Sweden. These two cultures agree in essential colony characteristics and in the pattern of their penicilli; the former, however, consistently produces more restricted and less heavily sporing colonies and shows penicilli generally smaller than the latter. In both strains, the penicilli are commonly borne as short branches on alternate sides of trailing or decumbent aerial hyphae in the manner characteristic of the *Penicillium fellutanum* sub-series.

Strain NRRL 2066, received in February 1946, from the Centraalbureau as a culture obtained by them as *Penicillium carmino-violaceum* Dierckx from the National Collection of Type Cultures, London, produces colonies which, in rate of growth and in general habit and color, are indistinguishable from NRRL 2064. Colony margins often show some aggregation of aerial hyphae into ropes or prostrate bundles and, in this regard, fit Biourge's description and figures for *P. carmino-violaceum* Dierckx. The conidia in this strain are about 2μ in diameter, globose with walls finely roughened, and so duplicate those of *P. roseo-purpureum;* conidia in *P. carmino-violaceum* were described and figured by Biourge as ovate to more or less elliptical. We believe that this culture should be regarded as representing *P. roseo-purpureum* despite the funiculose colony

margins, since individual strains are known to vary appreciably in this regard depending upon the substratum employed and other environmental factors.

Representative strains of *Penicillium roseo-purpureum* are occasionally isolated from soil and have been encountered among the isolates from deteriorating military equipment sent to us for identification. The species appears to be cosmopolitan, but not abundant, in nature.

The following species are believed to be inseparable from *Penicillium roseo-purpureum* Dierckx as that species is regarded here:

Penicillium carmino-violaceum Dierckx (Soc. Scient. Bruxelles **25:** 86. 1901. Biourge, Monograph, La Cellule **33:** fasc. 1, pp. 281–282; Col. Pl. X and Pl. XVI, fig. 93. 1923) is believed to approximate *P. roseo-purpureum* Dierckx as described above. Biourge's description reported some ropiness, and Thom's observations on his strain (Thom's No. 4733.28) records this character for the aerial growth but otherwise fails to provide adequate basis for distinguishing the species from *P. roseo-purpureum*. NRRL 733, cited by Thom in his Monograph (1930, p. 192) as No. 4733.83 and representative of *P. carmino-violaceum* agrees satisfactorily with *P. roseo-purpureum* as diagnosed above. It produces few conidial heads and develops some reddish pigmentation, especially in the exudate.

Citromyces sanguifluus Sopp (Monograph, pp. 115–117, Taf. XV, fig. 105; Taf. XXII, fig. 3. 1912) is believed to have represented a form approximating *Penicillium roseo-purpureum* Dierckx. Colonies were reported as tough, leathery, folded and wrinkled, producing loosely velvety, pale greenish conidial areas and exuding abundant blood red drops of exudate, with reverse at first yellowish red becoming deep red to almost black in age. Penicilli are figured as monoverticillate (approaching ramigenous) with conidia small, globose, and smooth. Biourge regarded the species as a synonym of *P. roseo-purpureum* Dierckx, a placement in which we concur.

Penicillium internum Morotchkovsky (Bul. Sci. Recueil Biol. Univ. Kiev. **2:** 78–79, fig. 8. 1936) is believed to represent a lightly colored form approximating *P. roseo-purpureum* Dierckx. The type has not been seen by us. A translation of the author's latin diagnosis follows: Colonies white, floccose; reverse uncolored or yellow; margin narrow, smooth; sterile hyphae hyaline, few septate, branched; conidiophores creeping, resembling sterile hyphae, more or less flexuous, branches 2.7 to 3.0μ in diameter, unseptate, minutely granulose within; sterigmata differing in form and size, 8.5 to 11.0μ by 2.0 to 2.5μ, mostly in two's or three's; conidia smooth, colorless, globose, 2.7 to 3.0μ, quickly falling away. Isolated from the fibrovascular bundles of the root of a sugar beet.

Occurrence and Significance

Members of the *Penicillium decumbens* series represent normal components of the mycoflora of most soils and commonly develop upon a wide variety of organic substrata if subjected to soil, dust, or water-borne contamination. They are world-wide in distribution, and appear to be unusually prevalent in tropical and subtropical areas. Since they grow so restrictedly in artificial culture, hence are easily overgrown and ob-

secured by more rapidly growing species, some question exists whether the number of strains isolated gives an adequate measure of their presence in nature. Species belonging to this group were especially abundant among the Penicillia isolated from various types of military equipment undergoing deterioration under field and test conditions. Little evidence is at hand which indicates a substantial and direct role in decay processes. It is suggested, however, that these forms may be able to gain an early foothold and hence pave the way for the invasion of subsequent and more destructive forms.

Macy and Steele (1934) included *Penicillium fellutanum* among molds studied as agents causing spoilage of butter. Van Beyma (1928b) reported *P. phaco-janthinellum* Biourge (regarded as *P. fellutanum* Biourge in this Manual) capable of destroying the tannin material "gambir" produced in Sumatra. Chrzaszcz and Tiukow (1931, 1932) reported *P. citreo-nigrum* (regarded as *P. citreo-viride* in this Manual) to produce good yields of citric acid.

Species belonging to this series have been occasionally implicated in diseases of plants, although little conclusive evidence of pathogenicity has been forthcoming. Sinha (1943) isolated *Penicillium fellutanum* from the surfaces of spoiled fruits in storage in Lucknow, India. *Penicillium decumbens* has been reported as common on grapes in Palestine, effecting damage through rot and a premature dropping of the berries. Morotchkovsky (1936), investigating the Penicillia isolated from stored sugar beet roots, reported two new species, *P. internum* and *P. necrosiferum*, which we believe are properly assignable to recognized members of the present series (see p. 220 and p. 218). Both were most common in necrotic peripheral fibrovascular bundles. Application of lime to the storage piles was found to effectively combat the Penicillia.

The pigmentation of certain members of this series is most striking, and some biochemical studies of the responsible pigments have been made. Posternak (1940 and 1941) reported a pigment ($C_{16}H_{12}O_6$) designated roseo-purpurine, to be produced by *Penicillium roseo-purpureum* Dierckx on a Czapek-Dox medium. The pigment is an anthroquinone and has the same general structure as citreo-roseine previously isolated from *P. citreo-roseum* Dierckx. It crystallizes as yellow needles, melts around 280°C., and, dissolved in carbonates, gives a red-brown color. Methods of isolation and identification are presented. The cultures were reported also to produce benzoic acid in the amount of *ca.* 20 mg./liter of culture medium. From cultures of *P. carmino-violaceum* Dierckx, grown upon a glycerol medium, Hind (1940a and b) isolated two anthroquinone pigments, $C_{16}H_{12}O_6$ and $C_{20}H_{16}O_7$, for which he proposed the names carviolin and carviolacin respectively. Both represented monomethyl ethers and

were indistinguishable in color. Carviolin is insoluble whereas carviolacin is somewhat soluble in cold water. Both are soluble in ethyl alcohol and acetone. Carviolin crystallizes as chrome colored needles, M.P. 286°. Carviolacin crystallizes as greenish fluorescent plates, M.P. 204° with a tendency to sublime above 185°. The preparation of various crystalline derivatives of these pigments was described. Ergosterol was extracted from the dried mycelium and recrystallized from alcohol.

Prior to this Krause and Ellis (1937), studying the inhibitory effects of ethyl and methyl alcohols on spore germination in different Penicillia, had reported two pigments to be produced by *Penicillium carmino-violaceum* and noted that one of these acted as an indicator. They did not, however, isolate or characterize these pigments, and their identity with those subsequently reported by Hind is open to question.

Penicillium restrictum Series

The *Penicillium restrictum* series is admittedly artificial in concept and is designed to cover certain forms which cannot otherwise be satisfactorily placed. Two species are included, namely: *P. restrictum* Gilman and Abbott and *P. fuscum* (Sopp) n. comb. Close relationship between the species included is not presumed, and they are considered together primarily as a matter of convenience. They do, however, show certain features in common, particularly coarsely roughened, globose conidia and a tendency to develop floccose colonies, which enables them to be keyed together and to be separated from the other monoverticillate Penicillia in the manner shown in the general key to this group (see p. 131).

Penicillium restrictum is of considerable interest because of its possible transitional position between the two genera, *Penicillium* and *Aspergillus*. Strains presenting the cultural and microscopical picture of a true monoverticillate *Penicillium* are sometimes observed. Structures associated with this specific name, however, are often produced by strains which, upon especially favorable media, produce conidial heads characteristic of *Aspergillus sydowi* in greater or less abundance. Thom and Raper, in their "Manual of the Aspergilli" (1945, p. 186), called attention to this occurrence and suggested that *P. restrictum* Gilman and Abbott should probably be assigned to the *A. versicolor* group along with *A. sydowi*. While we still regard this assignment as probably correct, we recognize that retention of the name is necessary to account for certain strains wherein the more complex, aspergilloid conidial apparatus does not appear and the smaller, fragmentary, penicillate structures characterize the culture.

Penicillium fuscum (Sopp) n. comb., as considered here, is believed to

approximate Sopp's *Citromyces fuscus*, although his species is known only from the original description since types were never distributed to other investigators. Consistent with Sopp's description, conidial areas are fuscous in age, conidiophores fairly long and characterized by limited vesicular enlargement, sterigmata are borne in a compact cluster suggestive of a simple *Aspergillus*, and conidia are large, globose, echinulate and brown. In our culture, conidiophore walls show a light yellow-brown color of the approximate shades seen in the *Aspergillus ustus* group. While clear evidence supporting such a view is not at hand, the possibility that *P. fuscum* may represent another species transitional in the direction of *Aspergillus* should not be overlooked.

Members of the series are typical soil organisms, and strains duplicating or approximating those cited in the text below have been isolated repeatedly in our laboratory over a period of many years. Such cultures commonly lose their capacity to produce abundant conidia and, being somewhat difficult to maintain in artificial culture, are often soon lost from collections. If long maintained, they commonly develop as practically nonsporulating, floccose growths hardly suggesting the original isolates except for the scattered production of conspicuously roughened globose spores.

Penicillium restrictum Gilman and Abbott, in Iowa State College Jour. Sci. **1:** 297, fig. 32. 1927. See also Thom, The Penicillia, pp. 176–177, fig. 20. 1930.

Colonies on Czapek's solution agar growing rather restrictedly, attaining a diameter of 2.0 to 2.5 cm. in 12 to 14 days at room temperature, azonate, appearing floccose, 1 mm. or more in thickness, consisting of a tough basal felt bearing a loose aerial mycelium of delicate hyphae, about 1.5 to 2.0μ in diameter, somewhat radially wrinkled in most strains, white or nearly so, bearing few conidial structures mostly after 1 week to 10 days (fig. 61A), conidia at first pale blue-green, shading quickly to dull gray (Ridgway, Pl. LII); exudate limited in amount, clear to pale yellow; odor none; reverse in yellow to peach or clay colors (R., Pl. XXIX); aerial hyphae developing numerous, short spur-like branches, some of which remain sterile, others of which bear conidia as isolated sterigmata, but which typically develop into conidiophores, mostly 25μ or less in length by 1.2 to 1.8μ in diameter, smooth-walled; penicilli consistently small, mostly monoverticillate or occasionally irregularly branched and sometimes showing one or two secondary penicilli on the same conidiophore; sterigmata often divergent, usually in small clusters up to 6 or 8 in number (fig. 61C), about 5.0μ by 1.5μ, narrowed at both ends with conidium-bearing tips

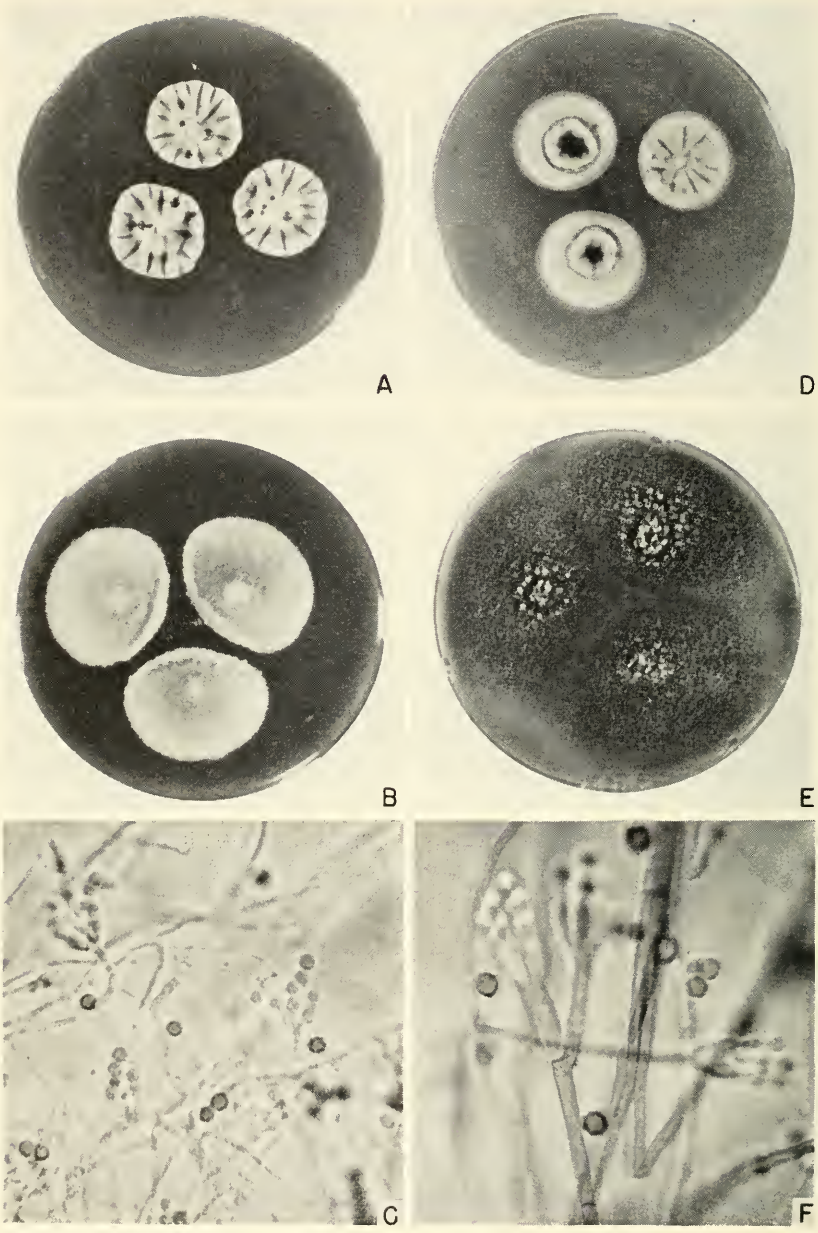


FIG. 61. *Penicillium restrictum* Gilman and Abbott, NRRL 1748 and *P. fuscum* (Sopp) n. comb., NRRL 721. *A* and *B*, Two-week-old colonies of *P. restrictum* on Czapek and malt agars. *C*, Detail of penicilli, × 1000; note very short conidiophores, limited sterigmata, and rough conidia. *D* and *E*, Two-week-old colonies of *P. fuscum* on Czapek and malt agars. *F*, Details of penicillus, × 1000; note roughness of conidia in this species also.

pointed; conidia globose, about 2.0 to 2.5μ, rarely 3.0μ in diameter with walls conspicuously roughened, not adhering in long chains.

Colonies on steep agar as described above but growing somewhat more rapidly, slightly heavier sporing, and producing more abundant exudate; penicilli as described above.

Colonies on malt agar restricted, deeply floccose, up to 2 mm., not furrowed, slightly heavier sporing (fig. 61B), appearing pale bluish gray throughout, darkest in sub-central areas; penicilli as described on Czapek.

Species diagnosis based upon Gilman and Abbott's original description, upon Thom's records of their type and a second strain, isolated from a peat bog by C. L. Shear (see Monograph, p. 177, 1930), and upon cultural studies of NRRL 1748 received in 1940 from Professor Elizabeth McCoy as a strain isolated by Professor E. M. Gilbert, in 1937, from Honduras soil.

Cultures presenting the cultural and morphological picture of this species are not infrequently encountered among soil isolates. They are maintained in culture with difficulty, however, and usually become sterile or nearly so after a limited number of transfers. Forms presenting the general aspect of the species, but known to represent atypical strains of *Aspergillus sydowi* (Bain. and Sart.) Thom and Church have been commonly observed. One such culture, obtained in 1936, and now maintained as NRRL 719, fits reasonably well the description of *Penicillium restrictum* when grown on Czapek's agar, but on malt agar develops as a fairly typical representative of *A. sydowi*. The latter species was among the most abundant of all molds isolated from deteriorating military equipment in tropical and subtropical areas. As submitted to us for identification, many of these strains when grown upon Czapek agar produced conidia on small and irregular penicillate structures, but, like NRRL 719, when grown on malt agar often developed as typical *A. sydowi*. The close relationship of these two species was discussed by Thom and Raper in their "Manual of the Aspergilli" (1945, p. 186). The validity of the species, *P. restrictum* Gilman and Abbott, remains somewhat in doubt, but it is included here to cover occasional isolates which cannot otherwise be satisfactorily diagnosed.

Citromyces griseus Sopp (Monogr., pp. 119–120, Taf. XV, fig. 104: Taf. XXII, fig. 5. 1912) is regarded as possibly having represented some form approximating *Penicillium restrictum* Gilman and Abbott, but by description differs in producing smooth conidia. A strain from the Centraalbureau received in March 1946, as *P. griseum* Olsen-Sopp originally from Professor Janke, Vienna, differs from *P. restrictum* as described above primarily in producing thinner and less definitely floccose colonies and conidia somewhat larger and coarsely roughened.

Penicillium fuscum (Sopp) n. comb.

Synonym: *Citromyces fuscus* Sopp, in Monograph pp. 120–122. Taf. XIV, fig. 100; Taf. XXII, fig. 6. 1912. See also, Thom, The Penicillia, p. 180. 1930.

Colonies on Czapek's solution agar growing slowly, attaining a diameter of 2.5 to 3.0 cm. in 12 to 14 days at room temperature, cushion-like, 1 to 2 mm. deep, spongy or fleshy, with surface often appearing wet in localized areas, showing light radial furrows in narrow submarginal zones, felted, showing some ropiness in central colony areas when viewed at low magnifications, becoming velvety in age in narrow marginal zones and with deep submerged mycelium extending 1 to 2 mm. beyond the edge of conidial development (fig. 61D), medium sporing throughout, heaviest in marginal and submarginal areas, at first olive-gray (Ridgway, Pl. LI) becoming deep grayish olive to hair brown (R., Pl. XLVI) in age; exudate lacking; odor slight or indefinite; reverse uncolored or nearly so; conidiophores variable, arising mostly from aerial hyphae and usually not exceeding 100μ in length by 2.0 to 2.5μ in diameter but occasionally longer up to 150 to 200μ, conspicuously septate, with walls comparatively heavy, light yellow-brown in color, smooth or finely roughened; penicilli variable, ranging from fragmentary to strictly monoverticillate to irregularly branched (suggesting the Divaricata), with two or more metula-like cells borne terminally or at lower septa; sterigmata divergent, in small clusters up to 6 or 8, not uncommonly in two's or three's and occasionally single, mostly 6 to 9μ by 2.0 to 2.5μ (fig. 61F), with conidium-bearing tips definitely constricted and comparatively long; conidia globose, at first colorless, spinulose, becoming coarsely roughened with prominent dark tubercles when mature, mostly 3.5 to 4.0μ or up to 4.5μ in diameter, olive-brown in mass, borne in tangled chains up to 50 to 100μ in length.

Colonies on steep agar growing more rapidly, about 4.0 cm. in 2 weeks, with texture and color as described above but somewhat heavier sporing; conidial structures as on Czapek.

Colonies on malt agar spreading broadly, up to 6.0 cm. or more in 2 weeks, comparatively thin, not spongy, with surface appearing somewhat velvety but characterized by abundant trailing and interlacing hyphae, heavily sporing throughout (fig. 61E), in dark olive-green shades; conidiophores somewhat longer than on Czapek and more frequently branched in the manner of the Divaricata.

The above diagnosis is drawn primarily from NRRL 721 isolated from Texas soil and sent to us in 1930 by Professor M. B. Morrow, University of Texas. The strain is identified with Sopp's *Citromyces fuscus* primarily upon the basis of its color, the character of its conidial structures, and its large coarsely roughened conidia. The change of name is dictated by inclusion of Wehmer's genus *Citromyces* in *Penicillium* (see p. 18). Correct

placement of the species remains somewhat in doubt, and assignment to its present position is based upon our belief that it can be keyed here more readily than elsewhere. Its possible closer relationship to the *Penicillium nigricans* series in the Divaricata should not be overlooked. If placed in that section it should be considered along with *P. albidum* Sopp. It differs from this form, however, in producing colonies not predominantly white, in its larger and more coarsely roughened conidia, and in the dark color of its conidiophores.

Occurrence and Significance

Forms approximating *Penicillium restrictum* G. and A. and *P. fuscum* (Sopp) are not infrequently encountered among molds isolated from soil. Their significance in nature is not known, and no studies of a biochemical nature based upon these species have come to our attention. Their chief interest lies in the fact that they possibly represent transitional forms connecting the Penicillia with the Aspergilli.

Penicillium adametzi Series

Outstanding Characters

Colonies consisting of a tough basal felt with surface growth usually somewhat floccose and regularly showing some development of hyphal ropes or funicles. Colony reverse often developing orange-red to brown or amber shades.

Conidiophores arising almost entirely from trailing aerial hyphae or ropes of hyphae, mostly as short perpendicular branches, normally less than 100μ in length and commonly much shorter.

Penicilli monoverticillate, rarely branched, consisting of terminal verticils of 5 to 10 or more sterigmata bearing conidia in tangled chains or fairly well defined columns.

Conidia globose or subglobose, mostly 2.0 to 3.0μ, with walls appearing granular or definitely roughened, in light yellow-green to gray shades.

Series Key

b. Colonies with funiculose habit predominant or well developed. . *P. adametzi* series
1′. Colonies usually developing dull reddish orange to brown shades in reverse.
aa. Conidia subglobose, 2.0 to 2.5μ, delicately granular. . . . *P. adametzi* Zaleski
bb. Conidia globose to subglobose, about 3.0μ in diameter, definitely rough *P. terlikowskii* Zaleski
2′. Colonies quickly developing deep vinaceous to purple colors in reverse and agar. . . . . Vinaceous sub-series
aa. Exudate abundantly produced, deep vinaceous, conidiophores short, rarely more than 50μ. . . . . *P. vinaceum* Gilman and Abbott
bb. Exudate lacking or limited, conidiophores longer, 200 to 250μ *P. phoeniceum* v. Beyma

Within the series, individual strains vary from essentially floccose, showing only a limited development of ropiness, to strongly funiculose with this character dominant in growing colonies. Strains likewise vary in the quantity of conidia produced and in the color of conidial masses. They further vary in the markings and to a lesser degree in the dimensions of conidia. Particular cultures may, therefore, differ rather markedly in their general appearance and characteristics. Zaleski (1928) studying the mycoflora of soils from coniferous forests in Poland, isolated a number of strains, and, apparently emphasizing differences rather than similarities, described at least four of these forms as representing new and separate species, namely: *Penicillium adametzi*, *P. niklewskii*, *P. paczoskii*, and *P. terlikowskii*. Careful comparison of his species descriptions and re-examination of his original cultures, as they have been maintained in our Collection and at the Centraalbureau in Baarn, fails to reveal adequate bases for recognition of all four species. These strains seem to fall into a graded series. Believing it to be most tangible, we have somewhat arbitrarily selected *P. adametzi* Zaleski as representative of the series and present a detailed description centered upon Zaleski's type of this species, but broadened sufficiently to include additional strains that are obviously closely related. *Penicillium terlikowskii* Zaleski is recognized to include forms in which ropiness is reduced and which produce conidia in fairly definite columns, somewhat larger and definitely roughened.

Members of the series show an unusual instability in artificial culture, often developing into "wet" and almost sterile strains after a few transfers. For this reason they tend to be quickly lost from collections.

Penicillium adametzi Zaleski, in Bul. Acad. Polonaise Sci: Math. et Nat. Ser. B, pp. 507–509; Taf. 47 and 61. 1927. See also, Thom, The Penicillia, pp. 194–195. 1930.

Colonies upon Czapek's solution agar growing fairly rapidly, 4 to 5 cm. in diameter in 14 days at room temperature, with mycelium forming a dense, tough, papery felt perhaps 500μ thick, buckled and more or less radiately wrinkled in the central area (figs. 63A and C), often becoming pronouncedly zonate in age, with conidial zones in pale yellow-green shades such as tea green to gnaphalium green (Ridgway, Pl. XLVII), with surface growth in the conidial areas characterized by the production of trailing simple hyphae and the development of prominent funicles or ropes of hyphae (fig. 62A), either prostrate, trailing, or ascending and sometimes elaborately branched, with conidiophores borne mostly as short perpendicular branches from individual hyphae or ropes of hyphae; reverse colorless to orange-yellow in shades such as tawny olive to Saccardo's umber (R., Pl. XXIX), with agar in lighter values of the same shades; exudate

lacking to fairly abundant, light amber in color; odor none or indefinite; conidiophores mostly borne as perpendicular branches from trailing hyphae

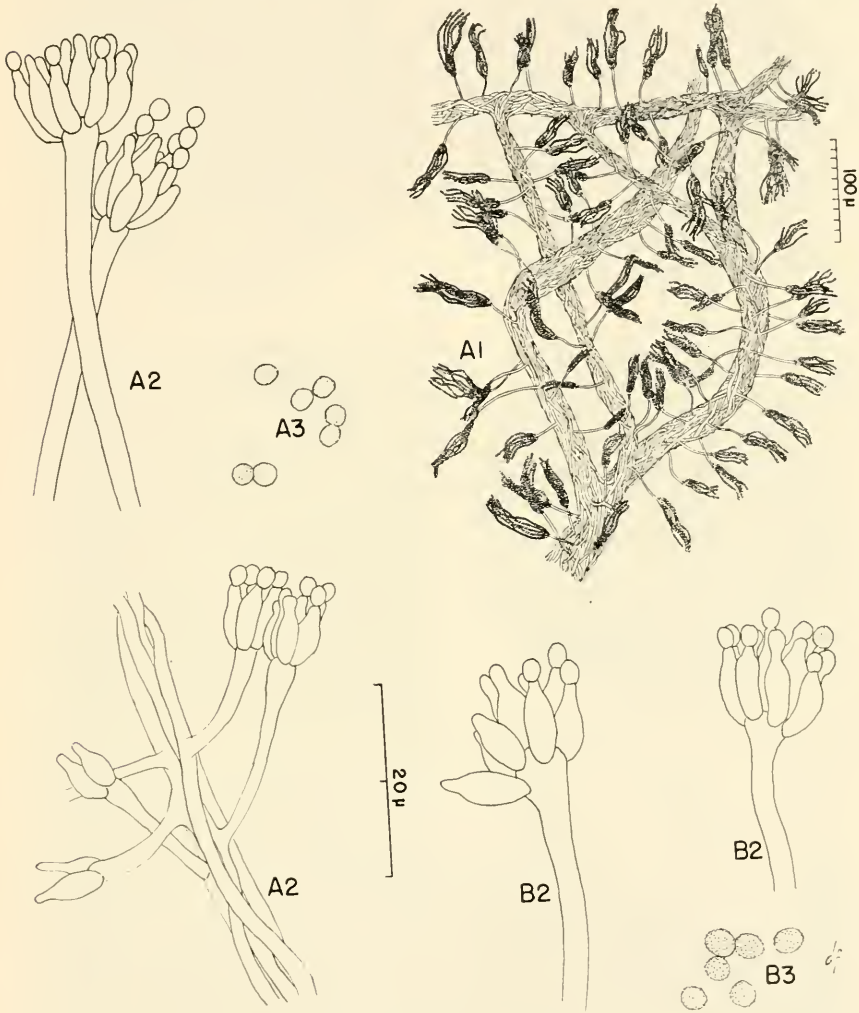


FIG. 62. *Penicillium adametzi* series. *A*, *P. adametzi* Zaleski: A_1, Habit sketch to show strongly funiculose habit of aerial hyphae and origin of conidial structures; A_2, Representative penicilli; and A_3 Mature conidia, × 1400. B_2, *P. terlikowski* Zaleski, representative penicilli; B_3, Mature conidia.

(fig. 63D), or ropes of hyphae (fig. 63E), short, commonly 20 to 30μ but up to 50μ by 1.5 to 2.0μ, occasionally longer and sometimes rising from submerged hyphae; penicilli monoverticillate, rarely showing one or two

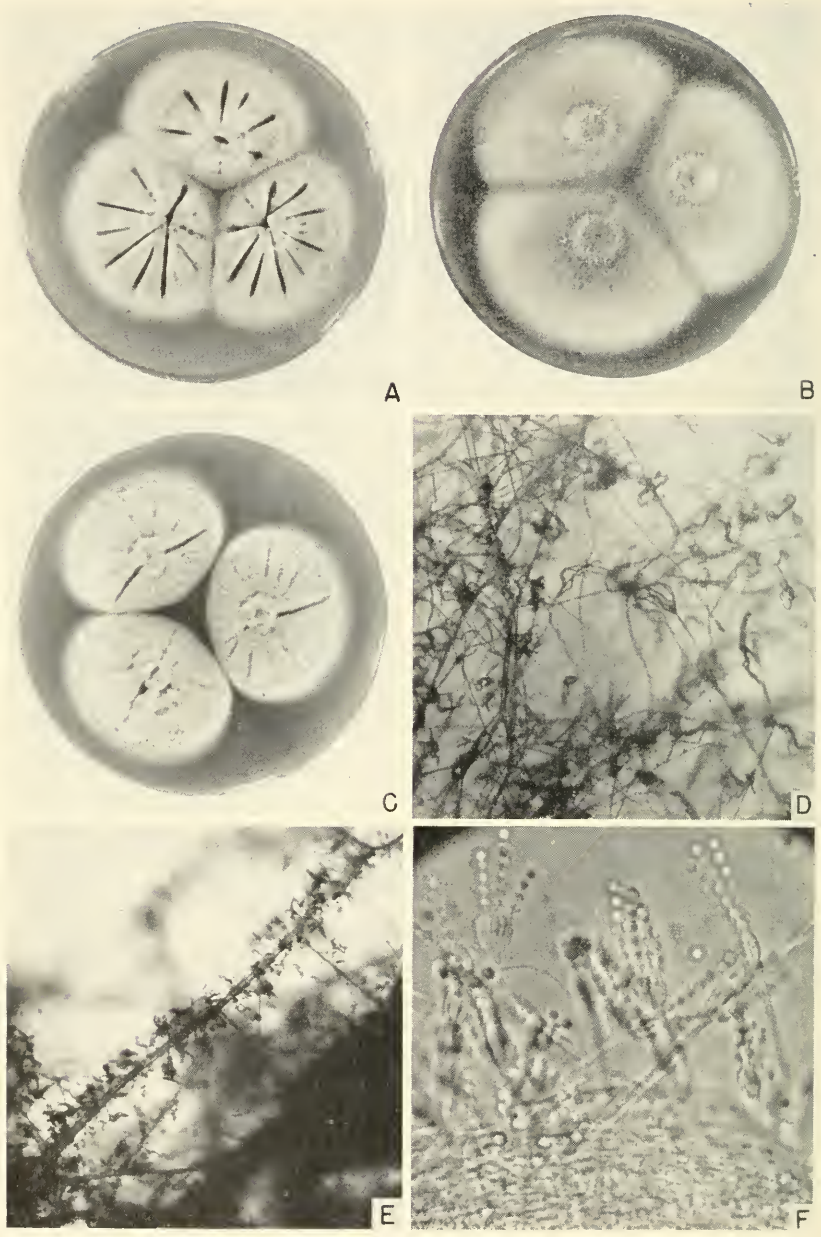


FIG. 63. *Penicillium adametzi* Zaleski. *A* and *B*, Two-week-old colonies of strain NRRl 737 on Czapek and malt agars. *C*, Strain NRRL 736 on Czapek. *D*, Low-power view of aerial growth in strain 737 showing limited ropiness, × 65. *E*, Strongly funiculose habit of strain 736, showing conidial structure arising as short branches from conspicuous hyphal ropes, or funicles, × 65. *F*, Portion of such a funicle greatly enlarged showing origin and detail of penicilli, × 900.

branches with secondary penicilli at lower levels, bearing conidia in tangled chains up to 50 to 100μ in length; sterigmata few in the verticil, numbering about 5 to 8, mostly 5 to 6.5μ by 2μ (figs. 62A$_2$ and 63F); conidia subglobose, about 2.0μ or 2.5μ, with walls appearing delicately granular.

Colonies upon steep and malt agars growing somewhat more rapidly than upon Czapek, less strongly wrinkled, more nearly floccose but with funiculose habit marked (fig. 63B), lighter sporing and with heavier conidial development in central rather than marginal areas; exudate lacking and colonies less strongly colored in reverse; penicilli often smaller but otherwise as described above; conidia appearing finely but definitely roughened.

Species description centered upon NRRL 737 received in 1928 from the Centraalbureau as Zaleski's type and discussed by Thom in his Monograph (1930) as No. 5010.1.

Strains showing colony and structural characteristics approximating NRRL 737 are commonly isolated from soil dilution plates and from materials subjected to soil or dust-borne contamination. Specific strains are commonly marked by individual differences, particularly in regard to the degree of ropiness, without showing adequate bases for separation.

A culture, received in February 1946 from the Centraalbureau as Zaleski's type strain, appears pathological and consistently produces colonies with a "wet" appearance; there are networks of sterile hyphae and ropes of hyphae but only distorted fruiting structures. While the original organism may be present, the strain no longer adequately represents the fungus described and figured by Zaleski (1928). NRRL 738, collected by Professor M. B. Morrow from Texas soil, has the general appearance and structures of *Penicillium adametzi* but produces a more compact mycelium presenting a surface almost velvety at the margin and closely and radiately wrinkled.

Penicillium niklewskii Zaleski (Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 504–505; Taf. 60. 1927.) as originally described differed little from *P. adametzi* of the same author. As examined by Thom and reported in his Monograph (1930), *P. niklewskii* was more strongly funiculose, producing "bristly, prostrate and ascending ropes or coremia of hyphae, . . . conidiophores mostly short branches from the funiculose or fasciculate bundles of hyphae". The penicilli did not differ significantly from those of *P. adametzi*. NRRL 736 previously maintained in our Collection as *P. niklewskii* is believed to comply with Zaleski's concept of that species, but the species is not regarded as sufficiently different from *P. adametzi* to warrant continued recognition.

Penicillium terlikowskii Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 501–502; Taf. 59. 1927. See also Thom, The Penicillia, pp. 203–204. 1930.

Colonies on Czapek's solution agar growing rather restrictedly, attaining a diameter of 2.5 to 3.0 cm. in 12 to 14 days at room temperature,

buckled and wrinkled with central area commonly raised, 1.0 to 2.0 mm. deep, consisting of a tough basal felt overlaid by a floccose to somewhat funiculose aerial mycelium composed of trailing and interlacing hyphae and ropes of hyphae, growing margin white (fig. 64A), about 1.0 to 2.0 mm. wide, fimbriate, medium to heavy sporing throughout or in some strains in marginal areas only, in dull gray shades near mineral gray

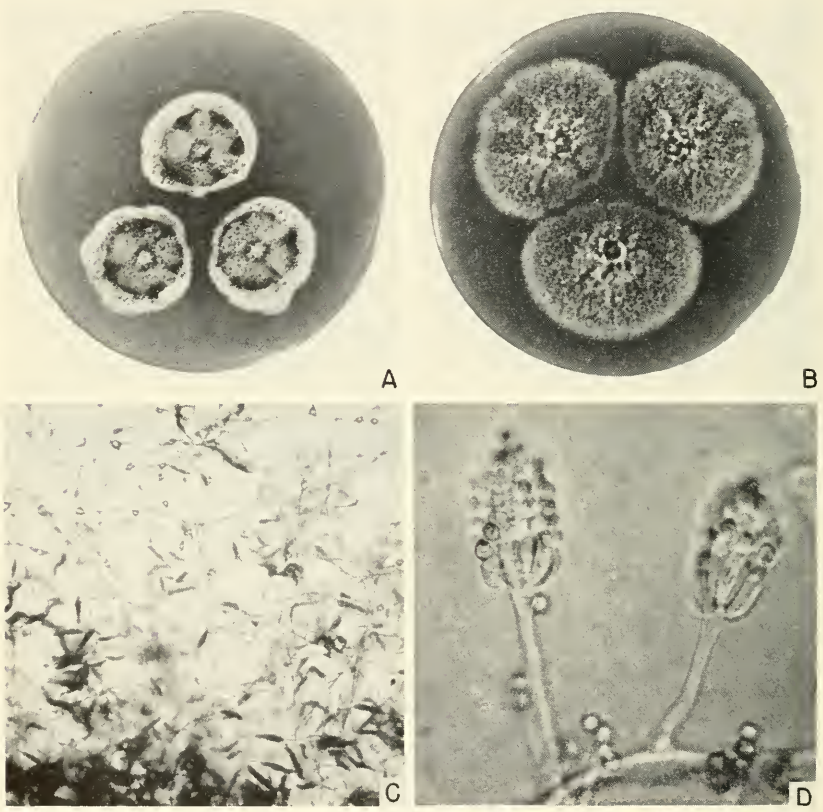


FIG. 64. *Penicillium terlikowskii* Zaleski, NRRL 2067. *A* and *B*, Two-week-old colonies on Czapek and malt agars. *C*, Low-power view of aerial growth, × 65. *D*, Detail of penicilli, × 900.

(Ridgway, Pl. XLVII) to olive-gray (R., Pl. LI); exudate fairly abundant, mostly as small droplets adherent to the mycelium, dull amber; odor lacking or indefinite; reverse in orange-red or red-violet to brown shades; conidiophores abundantly produced, arising primarily as short branches from aerial hyphae or ropes of hyphae (fig. 64C), commonly less than 100μ in length, occasionally longer by about 2.0μ, with walls apparently smooth but appearing granular within; penicilli monoverticillate, rarely branched,

consisting of a terminal verticil of 5 to 10 or more sterigmata, mostly 7.0 to 9.0μ by about 2.0μ (figs. 62B and 64D), parallel, crowded in the verticil with conidium-bearing tips definitely narrowed, producing chains of conidia up to 50μ or more in length in loose to well-defined columns; conidia subglobose to globose, mostly 2.5 to 3.3μ in diameter, with walls definitely roughened.

Colonies on steep agar growing more rapidly, about 5.0 cm. in 12 to 14 days, otherwise as described on Czapek except lacking the raised area in colony center and showing a somewhat deeper overgrowth of floccose to funiculose aerial mycelium; reverse and details of conidial structures as described above.

Colonies on malt agar about 3.0 to 4.0 cm. in 12 to 14 days, plane, with growing margin wider, about 2.0 to 3.0 mm., more definitely fimbriate than on Czapek and steep agars, heavily sporing throughout, in yellow-green shades near Andover to dull ivy green (R., Pl. XLVII) with a thin superficial growth of white aerial mycelium (fig. 64B), reverse in dull flesh to light orange shades; microscopic details as described on Czapek except sterigmata more numerous in the verticil, up to 15 or 20, and conidia in well defined columns up to 300μ in length.

Species description centered upon NRRL 2067, received in December 1945, as No. 241 from P. W. Brian, Imperial Chemical Industries, Ltd., Bracknell, England; and NRRL 752, received in 1928 from the Centraalbureau as Zaleski's type. Strain NRRL 2067 is given priority in citation since we believe this strain more nearly represents Zaleski's species as originally described and as discussed by Thom in his Monograph (1930). Strain NRRL 752 is still regarded as representative of the species but after years of laboratory cultivation fails to completely satisfy the original diagnosis.

Penicillium terlikowskii Zaleski is regarded as belonging in the *P. adametzi* series but occupying a rather terminal position, since it represents something of an extreme in the variation normally encountered in the series. Conidia are somewhat larger than in *P. adametzi*, are more definitely roughened, and characteristically occur in more or less well-defined columns. Colonies show the basic characteristics of *P. adametzi* but are generally less definitely funiculose. Like other members of the series, the species may be regarded as typically a soil form.

Penicillium paczoskii Zaleski (Bul. Acad. Polonaise Sci.: Math. et Nat. Ser., B, pp. 505–506–507; Taf. 47, 61. 1927) as originally described and as reported by Thom in his Monograph (1930) apparently represented a form approximating, or closely related to, *P. terlikowskii* Zaleski as described above. Colonies were described as raised, velvety cushions, transiently bluish green to dusky olive-green, consisting of an aerial growth of trailing hyphae and ropes of hyphae. Conidiophores ranged up to 100 or 200μ and bore monoverticillate penicilli producing loose columns of spores up to 200μ in length. Conidia were reported as subglobose, about 3.0μ in diameter,

smooth (*fide* Zaleski) or delicately punctate (Thom). NRRL 751, received in 1928 from the Centraalbureau as Zaleski's type, is believed to remain representative of Zaleski's original strain. A second substrain of his type, received from the same source in June 1946, duplicates NRRL 751 except colonies are more definitely funiculose and the conidia are generally globose rather than subglobose. Careful examination of the original description and of the cultures now available has failed to furnish adequate bases for the separation of *P. paczoskii* and *P. terlikowskii*. While the decision is recognized as somewhat arbitrary, it is believed that the latter should be recognized as the more distinctive species and the former considered as a synonym.

Penicillium jantho-citrinum Biourge (Monograph, La Cellule **33**: fasc. 1, pp. 311–313; Col. Pl. IX, Cart. 1, Pl. XV, fig. 90. 1923) possibly represented a species approximating *P. terlikowskii* Zaleski. No culture of this species was received by Thom in 1924, hence no assignment was made in his Monograph (1930). A strain bearing this label was received from the Centraalbureau in May 1946, as a culture from Biourge in 1929. This strain duplicates, essentially, NRRL 751 (see above). If the strain from Baarn can be assumed to represent Biourge's species, *P. jantho-citrinum* should be regarded as belonging with *P. terlikowskii*. The original description and figures are inadequate to warrant recognition of this species, in preference to *P. terlikowskii*, despite the priority of the name.

Vinaceous Sub-Series

Two species are included, *Penicillium vinaceum* Gilman and Abbott and *P. phoeniceum* v. Beyma, both of which are characterized by the production of intense vinaceous to purple pigmentation in the colony reverse and in the surrounding agar.

In rate of growth, in colony habit and texture, and in details of structure, *Penicillium vinaceum* is strongly suggestive of the species that comprise the *P. adametzi* series proper. Colonies are floccose-funiculose, conidiophores are generally borne as short branches from aerial hyphae or ropes of hyphae, and penicilli are comparatively small. It differs from *P. adametzi* and *P. terlikowskii* markedly, however, in producing highly pigmented colonies with profuse exudate and colony reverse in deep vinaceous shades.

Penicillium phoeniceum, while possibly not closely related to the above genetically, produces an intense red-violet to purple pigmentation in colony reverse. Unlike *P. vinaceum*, conidiophores of *P. phoeniceum* arise primarily from the substratum or the basal felt, and little or no exudate is normally produced. The species is keyed with *P. vinaceum* primarily as a matter of convenience.

Penicillium vinaceum Gilman and Abbott, in Iowa State College Jour. Sci. **1**: 299, fig. 34. 1927. See also Thom, The Penicillia, pp. 195–196, fig. 23. 1930.

Colonies on Czapek's solution agar (Col. Pl. IV) growing rather restrictedly, attaining a diameter of 2.0 to 2.5 cm. in 10 to 12 days, strongly fur-

rowed in a predominantly radial pattern, comparatively deep, up to 1.0 to 1.5 mm., with margin fairly abrupt, showing some funiculose arrangement of vegetative hyphae (fig. 65A), with mycelium light gray to light vinaceous gray in age, generally light sporing throughout and heavier sporing in marginal areas of crowded colonies, pale gray-green approxi-

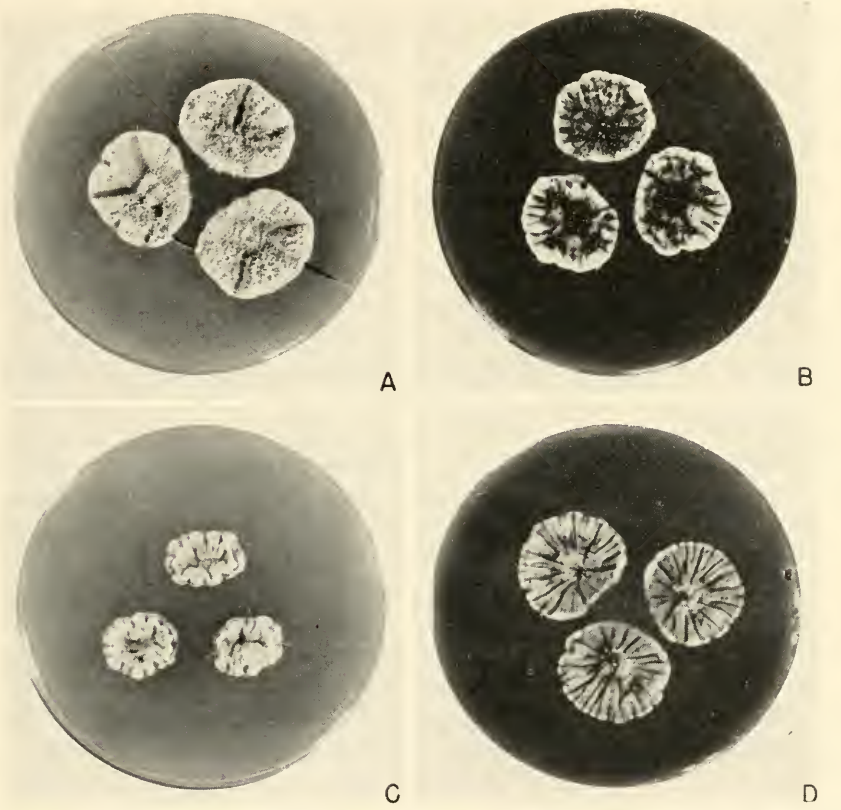


FIG. 65. *A* and *B*, *Penicillium vinaceum* Gilman and Abbott, NRRL 739, on Czapek and steep agars at two weeks; note the abundant vinaceous exudate on steep. *C* and *D*, *P. phoeniceum* v. Beyma, NRRL 2070, on Czapek and steep agars. Both species are strong pigment producers and quickly discolor the substratum, particularly when grown on steep agar.

mating light mineral to mineral gray (Ridgway Pl. XLVII); exudate abundantly produced, often collecting in large drops, in pale to deep vinaceous shades, usually characterizing the colony and producing the predominant color effect; odor slight or lacking; reverse in vinaceous shades (R., Pl. XXVII) through hellebore red to deep hellebore red (R., Pl. XXXVIII) to deep red-violet shades near violet carmine to burnt lake

(R., Pl. XII) in age, with surrounding agar colored in similar but less intense shades; conidiophores usually borne from aerial hyphae, short, rarely more than 50μ in length by 1.5 to 2.0μ in diameter, apparently smooth-walled, mostly unbranched but occasionally producing diverging branches suggestive of the *Penicillium janthinellum* series; penicilli usually strictly monoverticillate, usually consisting of a limited verticil of 5 to 8 sterigmata; sterigmata 6.0 to 7.5μ by 1.5 to 2.0μ with apices narrowed, somewhat divergent; conidia globose to subglobose when ripe, with ends sometimes apiculate during development, mostly 2.0 to 2.5μ, occasionally 3.0μ in diameter with walls appearing slightly irregular or in some strains definitely roughened.

Colonies on steep agar essentially as above but generally showing more vinaceous purple in the vegetative mycelium and producing abundant exudate in deeper vinaceous purple shades (fig. 65B); reverse as on Czapek but generally darker; conidial structures as described above.

Colonies on malt agar growing restrictedly, more or less floccose up to 2.0 to 2.5 mm. deep in central area, dull gray-buff in color; light sporulating throughout; exudate lacking or very limited in amount and not definitely vinaceous; reverse in brown shades rather than vinaceous and not coloring the surrounding agar; conidial structures as described above.

Species description centered upon Gilman and Abbott's type, NRRL 739, received in 1927 by Thom and subsequently maintained in his collection as No. 4894.15. This culture was originally isolated from Utah soil. Additional strains, duplicating the above in essential characters, but showing strain variation, have been occasionally encountered. NRRL 2063, received in June 1945, from Professor G. W. Martin (Jeffersonville Quartermaster Depot, No. J 774) as a strain isolated from the sidewall of a tent in the area of Hollandia, New Guinea, represents an extreme type by producing conidia that are conspicuously echinulate and strongly suggestive of those produced by the *Penicillium nigricans* series. In colony characteristics, this culture duplicates NRRL 739 almost exactly. Penicilli are generally monoverticillate but more frequently branched than in Gilman and Abbott's type. On malt agar, small rounded masses of thick-walled cells, 50 to 80μ in diameter, suggesting sclerotia normally develop.

Penicillium phoeniceum van Beyma, in Zentbl. f. Bakt., etc., (II) **88:** 136–137, figs. 4 and 5. 1933.

Colonies on Czapek's solution agar growing very restrictedly (fig. 65C), about 1 cm. in 10 to 12 days, raised, cushion-like, 1.0 to 1.5 mm. deep, consisting of a tough felt with surface growth somewhat floccose or funiculose, azonate, tending to develop radial furrows, with growing margin thin, largely submerged, about 1 mm. wide, and with agar slightly de-

pressed, light sporing, central areas white or in light pink shades and marginal areas 1 to 2 mm. wide developing pale blue-green shades; exudate lacking or limited in amount; odor none; reverse quickly developing bright red-violet shades, becoming dark purple in age (Ridgway, Pl. XXXVII), with surrounding agar similarly and, at length, intensely colored; conidiophores usually erect, arising primarily from the substratum or the basal felt, up to 200 to 250μ long by 2.0 to 2.5μ, with walls smooth or delicately roughened, enlarging slightly near the apex, usually unbranched but occasionally once-branched in the terminal area; penicilli monoverticillate, consisting of simple verticils of sterigmata, from 5 to 10 or 12 in number, roughly parallel or slightly divergent, bearing conidia in tangled chains; sterigmata mostly 8 to 10μ by about 2.0μ, occasionally up to 12 or 14μ in length, gradually tapering to the conidium-bearing tips; conidia appearing somewhat elliptical or apiculate when first formed, becoming globose to subglobose at maturity, mostly 2.5 to 3.0μ in diameter, with walls smooth or finely granular.

Colonies on steep agar restricted but growing more rapidly than on Czapek, about 1.5 to 2.0μ in 10 to 12 days, raised, cushion-like, 1 to 2 mm. deep, often becoming narrowly zonate, closely furrowed in a radial pattern with colony texture and surface as above (fig. 65D), somewhat heavier sporing, in dull gray-green shades near mineral gray to tea green; reverse as on Czapek but more quickly and intensely colored; conidial structures as described above.

Colonies on malt agar up to 1.5 cm. in 10 to 12 days, with central area raised 1 to 2 mm., lightly furrowed, with surface appearing almost velvety but with abundant trailing hyphae and ropes of hyphae, growing margin thin, about 2 mm. wide, otherwise heavily sporing throughout, near mineral gray; colonies in reverse becoming brown in central areas, not showing any purple pigmentation or discoloration of the surrounding agar; conidial structures as described above but usually somewhat larger, bearing conidia in tangled chains up to 100μ in length.

Species description based upon van Beyma's type received in July 1946, from the Centraalbureau, and included in our Collection as NRRL 2070. The type strain was originally isolated from sooty mold of a palm (*Phoenix*) at Baarn, Holland.

This species is placed next to *Penicillium vinaceum* upon the basis of its general colony characteristics but is not regarded as closely related to that form. Colony surfaces on all media tend to show a floccose or funiculose development of aerial hyphae, and to produce an intense pigmentation on Czapek and steep agars. Unlike the other members of the general series to which it is assigned, conidiophores in *P. phoeniceum* arise almost entirely from the substratum or the basal felt, and rarely from ropes of aerial

hyphae. Colonies are also more restricted and produce little or no exudate.

Occurrence and Significance

Members of the present series appear to be abundant in all soils, particularly forms approximating *Penicillium adametzi*. Representative strains have been received from Professor G. R. Bisby from Manitoba soils, from Professor M. B. Morrow from Texas soils, and numerous other investigators making soil population studies. These species were commonly isolated in our work in the Division of Soil Microbiology, U. S. Department of Agriculture, Washington, D. C., and have been frequently encountered at this Laboratory in our search for penicillin-producing and other industrially useful molds. Not unexpectedly, members of the series have occasionally occurred among the isolates from deteriorating military equipment submitted for identification. The significance of these forms in decomposition processes has not been adequately investigated.

Penicillium terlikowskii Zal. has been shown to be an active producer of the antibiotic gliotoxin (Brian, 1946), and because of this characteristic, the species is believed to exert a marked effect upon the microbiological population of certain soils in which it is unusually prevalent. Brian, Hemming, and McGowan (1945) reported that the toxicity to mycorrhiza in Wareham Health soil was due to antibiotics, particularly gliotoxin produced by *Trichoderma viride* and certain strains of *Penicillium*, reported as *P. jenseni*. These latter strains, when examined by us, were diagnosed as more nearly representing *P. terlikowskii* Zal. Our identification was accepted and used in a subsequent report by Brian (1946). In this report, the influence of various substrate constituents and strain variation on gliotoxin production was discussed.

Sasaki (1939) reported *Penicillium jantho-citrinum* as the active pathogen in eleven cases of otomycosis, although the identification of the fungus is not verifiable.

Penicillium phoeniceum v. Beyma has been studied particularly with reference to the striking pigment which it produces. Friedheim (1933) reported a red pigment, phenicin, to be produced in the mycelium of this mold. The pigment in its red form was soluble in water but insoluble in ether or chloroform. When acidified the pigment turned yellow and could then be extracted with the above solvents and from them with $NaHCO_3$. The pigment was found to increase respiration 200–300 percent when added to a suspension of washed, non-pigmented *Bacillus pyocyaceus* (= *Pseudomonas aeruginosus*) cells. In a subsequent paper (1938), yields of 44 mg. pigment were reported from 3.5 gms. mycelium produced in

100 ml. of culture medium, and the pigment was referred to as phoenicine. Posternak (1938) reported phenicin ($C_{14}H_{16}O_6$) to be a ditoluquinone, M.P. 230–231°C., which gave yellowish red solutions at pH 1.6 to 3.5 and reddish violet at pH 4.9 to 6.0. Composition and various derivatives of the pigment were discussed. Curtin, Fitzgerald, and Reilly (1940) found a specially modified Czapek-Dox medium containing 3.0 gm. $NaNO_3$, 0.3 gram $MgSO_4 \cdot 7H2$, and 50 gm. glucose per liter to be most favorable for phoenicine production. They reported a culture received from the Centraalbureau as *Penicillium rubrum* Grassberger-Stoll to be $2\frac{1}{2}$ to 3 times more productive than *P. phoeniceum* v. Beyma, and yields of pigment up to 2.0 gm. per 11.4 gm. of mycelium were obtained. Bitancourt (1941) reported *P. phoenicum* as common on rancid and rotting Brazil nuts in storage.

The Ramigena Series

Outstanding Characters

Colonies usually restricted, close-textured and consisting of a compact basal felt with surface appearing velvety or nearly so, often light sporing during the first 8 to 10 days; sometimes broadly spreading, tending to be floccose, and ranging from light to heavy sporing.

Conidiophores (fertile hyphae) prostrate or ascending, arising from the substratum or from creeping aerial hyphae, typically branched, with branches either 1-celled (metula-like) or long and septate, usually unequal in length, simple or rebranched, not producing definite apical verticils of metulae or branchlets.

Penicilli typically monoverticillate, borne terminally on the extremities of the branched conidiophores. Individuality of the monoverticillate penicillus is usually clearly evident, but repeated divaricate branching at various levels precludes definiteness of organization or arrangement.

Conidia are typically small, but range from globose to strongly elliptical, and from smooth-walled to definitely roughened, depending upon the species.

Series Key

B. Conidiophores mostly branched, occasionally rebranched, each bearing a terminal monoverticillate penicillus but not arranged as a definite apical verticil of metulae (or branchlets).....Ramigena series

1. Colonies growing restrictedly upon all media, mostly 1.5 to 2.5 cm. diameter in 10 to 12 days.

a. Conidia definitely elliptical, smooth-walled.

1′. Conidial areas in gray-green shades, with conidia strongly elliptical to narrowly cylindrical, with ends broad, not pointed

P. capsulatum Raper and Fennell

2′. Conidial areas in blue-green shades with conidia elliptical and with ends somewhat pointed ..... *P. cyaneum* (B. and S.) Biourge

b. Conidia globose, ovate, or slightly elliptical and with walls roughened.

1′. Conidia globose or nearly so, in divergent chains, not forming columns *P. waksmani* Zaleski

2′. Conidia ovate to slightly elliptical, in parallel chains forming compact columns ..... *P. charlesii* Smith

2. Colonies growing more rapidly upon most media, usually 4.0 to 5.0 cm. diameter or more in 10 to 12 days.

a. Conidia rough, echinulate; colonies vinaceous to reddish brown in reverse. *P. velutinum* v. Beyma

b. Conidia smooth; colonies developing yellow in reverse ... *P. citrinum* series (see The Velutina pp. 338–354)

This series includes a number of forms, first described and figured by Bainier and Sartory (1912, 1913) as species of *Citromyces*, in which the monoverticillate type of penicillus is characteristically produced, but in which the fertile hyphae, instead of developing as erect conidiophores tipped by single penicilli, usually appeared as creeping or ascending fertile hyphae bearing branches from several septa. They vary in complexity from simple penicilli to structures bearing verticils of fruiting cells (or metulae) near the apices of the main axes (fig. 66A and B).

Cultures originally obtained from the Bainier collection under the names published by Bainier and Sartory failed to comply with their descriptions to such a degree that Thom (1930) questioned whether he had received authentic cultures of any of them. Bainier and Sartory's descriptions appear to have been based upon colonies grown upon licorice sticks, hence failed to include adequate data regarding colony characters. Thom's own collections, and those of other investigators, however, showed that there were in nature abundant forms which produced branching fertile hyphae, with each branch terminating in a typical monoverticillate penicillus. In his Monograph, Thom (1930) recognized these irregularly branched forms as composing a separate and intermediate group, the Monoverticillata-Ramigena, between the true monoverticillates, or the Monoverticillata-Stricta, and the simpler biverticillate forms such as *Penicillium corylophilum* Dierckx and *P. citrinum* Thom. Some additional species have been described since that time. Continued study has led us to reconsider this arrangement, and we now believe that these forms should be regarded as constituting a recognizable series within the true Monoverticillata since they d ffer from the more usual forms principally in the ramigenous character of their conidiophores.

As understood by us, the series contains five well marked species, with primary separation based upon the general rate and character of colony

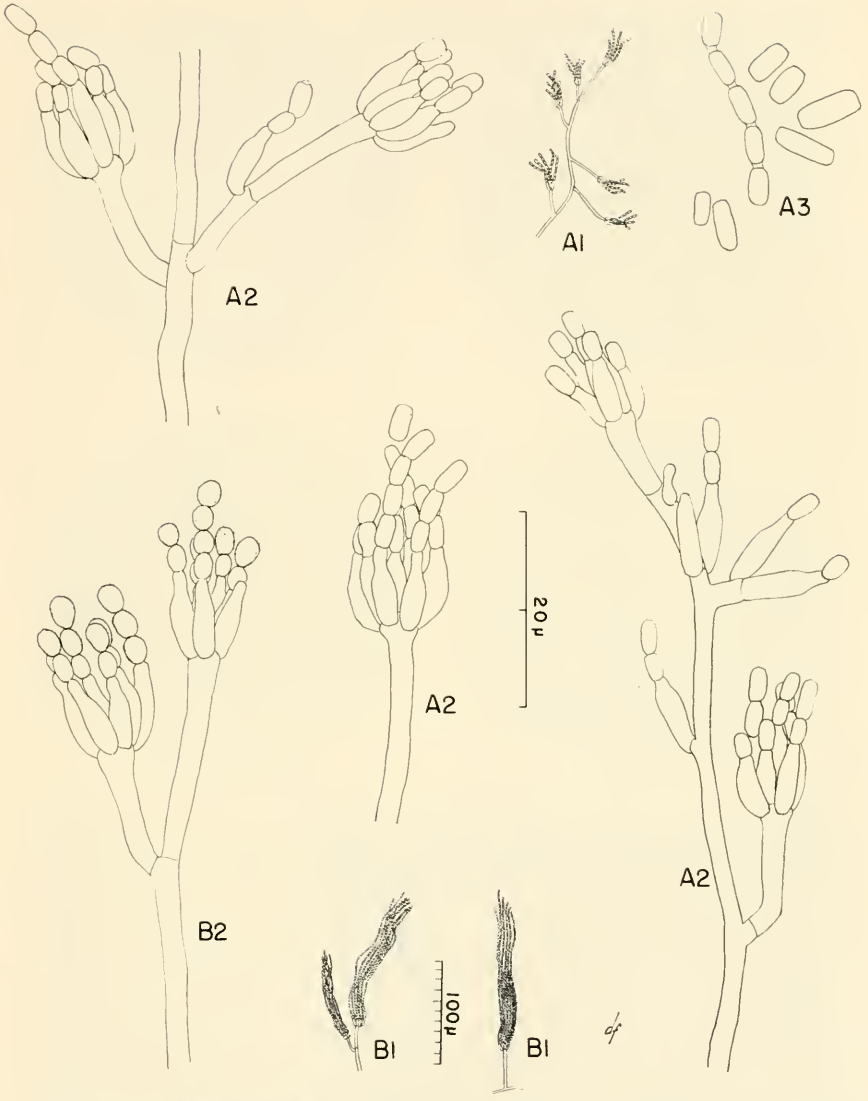


FIG. 66. *A*, *Penicillium capsulatum* Raper and Fennell: A_1, Habit sketch showing ramigenous origin of penicilli; A_2, Representative penicilli showing the irregularity of patterns encountered; A_3, Mature conidia showing their persistent cylindrical to capsular shape, × 1400. *B*, *P. charlesii* Smith: B_1 Habit sketches of penicilli; B_2, Enlarged view of typical branched conidial structure.

growth, and with secondary separation based upon the shape and wall-character of the conidia.

Penicillium capsulatum Raper and Fennell, in Mycologia **40:** 528–530, fig. 7. 1948.

Colonies on Czapek's solution agar growing restrictedly, attaining a diameter of 1.5 to 2.0 cm. in 10 to 12 days at room temperature, consisting of a comparatively thin, close-textured mycelial felt, tough, tearing irregularly, with surface appearing velvety or very slightly floccose, deeply furrowed (fig. 67A and D), commonly raised or depressed in central area, azonate in most strains, with growing margin narrow, about 1 mm. wide, white, medium sporing throughout, in gray-green shades, at first approximately court gray or gnaphalium green (Ridgway, Pl. XLVII) becoming darker in age near sage green (R., Pl. XLVII), exudate lacking; odor lacking or indefinite; reverse uncolored or slightly greenish at first but later showing orange to pinkish shades; conidiophores ascending, arising primarily from creeping or interlacing hyphae (fig. 67E), from very short up to 100μ or more in length by 2.0 to 2.5μ in diameter, walls smooth, branching irregularly, occasionally over their entire length, but more abundantly in terminal areas; penicilli monoverticillate, borne on branches of varying length and occasionally more or less clustered but consistently retaining their individual character (fig. 67F); sterigmata borne irregularly but typically in simple clusters, ranging from 4 to 5 up to 8 to 10 in the verticil, usually crowded, parallel, sometimes divergent, mostly 8 to 10μ by 2.0 to 2.2μ but not infrequently larger or smaller; conidia strongly elliptical, commonly capsule-shaped, mostly 3.0 to 4.0μ by 2.0 to 2.5μ, but frequently larger, with walls smooth.

Colonies on steep agar growing more rapidly, 2.5 to 3.0 cm. in 10 to 12 days, texture as described above but more strongly and deeply furrowed (fig. 67B), heavier sporing throughout, at first near pea green becoming sage green in colony center (R., Pl. XLVII); exudate limited, pale yellow; odor sourish; reverse uncolored or in yellow shades; conidiophores and penicilli as described above; conidia more consistently capsule-shaped.

Colonies on malt agar about 2.5 to 3.0 cm. in 10 to 12 days, comparatively thin with center commonly raised, velvety, heavily sporing throughout (fig. 67C), pea green to sage green, reverse in dull yellow to drab shades; conidiophores longer up to 200 to 300μ and loosely branched, commonly arising from the substratum, with walls smooth but appearing granular within; penicilli more regular in pattern than on Czapek or steep agar, usually consisting of a closely crowded cluster of 6 to 12 or more parallel sterigmata, 7 to 8μ by 1.5 to 2.0μ, bearing conidia in long parallel chains forming compact columns, about 10μ in diameter and up to 150μ or more in length; conidia very strongly elliptical to narrowly cylindrical, mostly 3.0 to 4.0μ by 1.5 to 2.0μ, occasionally up to 6.0 or 7.0μ by 2.0 to

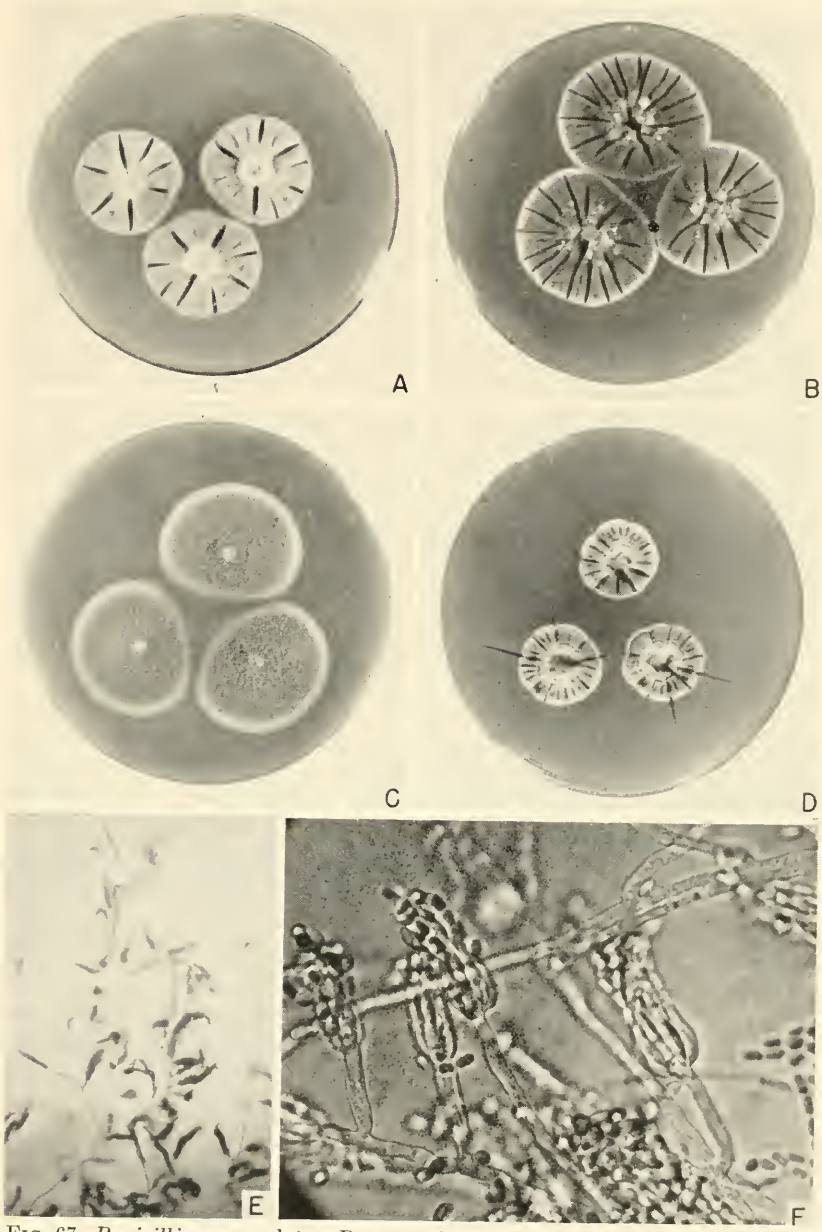


FIG. 67. *Penicillium capsulatum* Raper and Fennell. *A*, *B*, and *C*, Two-week-old colonies of strain NRRL 2056 on Czapek, steep, and malt agars, respectively. *D*, Strain NRRL 2057 on Czapek agar, illustrating normal variation within the species. *E*, Low-power view showing origin of conidial structures from ascending hyphae, × 100. *F*, Detail of penicilli, × 900.

3.0μ, with walls smooth, adhering in long chains when viewed in fluid mounts.

The binomial *Penicillium capsulatum* was assigned to the species because of the characteristically strongly elliptical to narrowly cylindrical form of its conidia.

Species description centered upon NRRL 2056 received in September 1945, from Professor W. H. Weston, Harvard University, as a culture isolated in the Panama Canal Zone from an optical instrument by Dr. W. G. Hutchinson. It is duplicated also by NRRL 2057, received in May 1945, from Dr. W. Lawrence White, Philadelphia Quartermaster Depot as a strain isolated from exposed canvas in the Gilbert Islands.

Additional strains representing this species have been repeatedly encountered among the molds isolated from deteriorating military equipment in tropical and sub-tropical areas. No information is available regarding the extent of growth or the amount of damage caused by this organism, but its repeated isolation from such sources would seem to indicate its probable wide distribution in tropical and subtropical soils.

Penicillium cyaneum (B. and S.) Biourge, in Monograph, Liste Onomastique, La Cellule **33:** fasc. 1, p. 102. 1923. Emend. Thom, in The Penicillia, pp. 226–228. 1930.

Synonym: *C. cyaneus* Bainier and Sartory, in Bul. Soc. Mycol. France **29:** 157–161; Pl. IV, fig. 4. 1913.

Colonies on Czapek's solution agar growing restrictedly, reaching a diameter of 2.5 to 3.0 cm. in 12 to 14 days at room temperature, consisting of a close-textured basal felt, radially furrowed, with central or subcentral areas commonly raised, surface appearing almost velvety or somewhat floccose from a limited growth of sterile aerial mycelium (fig. 68A), at first azonate or nearly so but sometimes becoming broadly zonate in age, light to medium sporing, varying in color from pale dull glaucous blue near the margin to deep bluish gray-green (Ridgway, Pl. XLII) in central areas; exudate lacking or limited, clear to cinnamon; odor none; reverse colorless or becoming yellowish to rosy in age; conidiophores 100 to 200μ by 2μ, arising separately from the substratum or as branches from ascending aerial hyphae, with walls smooth, irregularly branched, occasionally bearing definitely terminal groups of penicilli; penicilli monoverticillate, small, usually consisting of closely crowded verticils of 5 to 8 parallel sterigmata, producing narrow, loose columnar masses of conidia up to 100μ in length; sterigmata 7 to 9μ by 2.0 to 2.2μ, with larger or smaller cells not uncommon; conidia elliptical, mostly 3.0 to 4.0μ by 2.0 to 2.5μ, with ends often more or less pointed, smooth-walled.

Colonies on steep agar 2.5 to 3.0 cm. in 12 to 14 days at room temperature, slightly deeper and more closely wrinkled than on Czapek, appearing

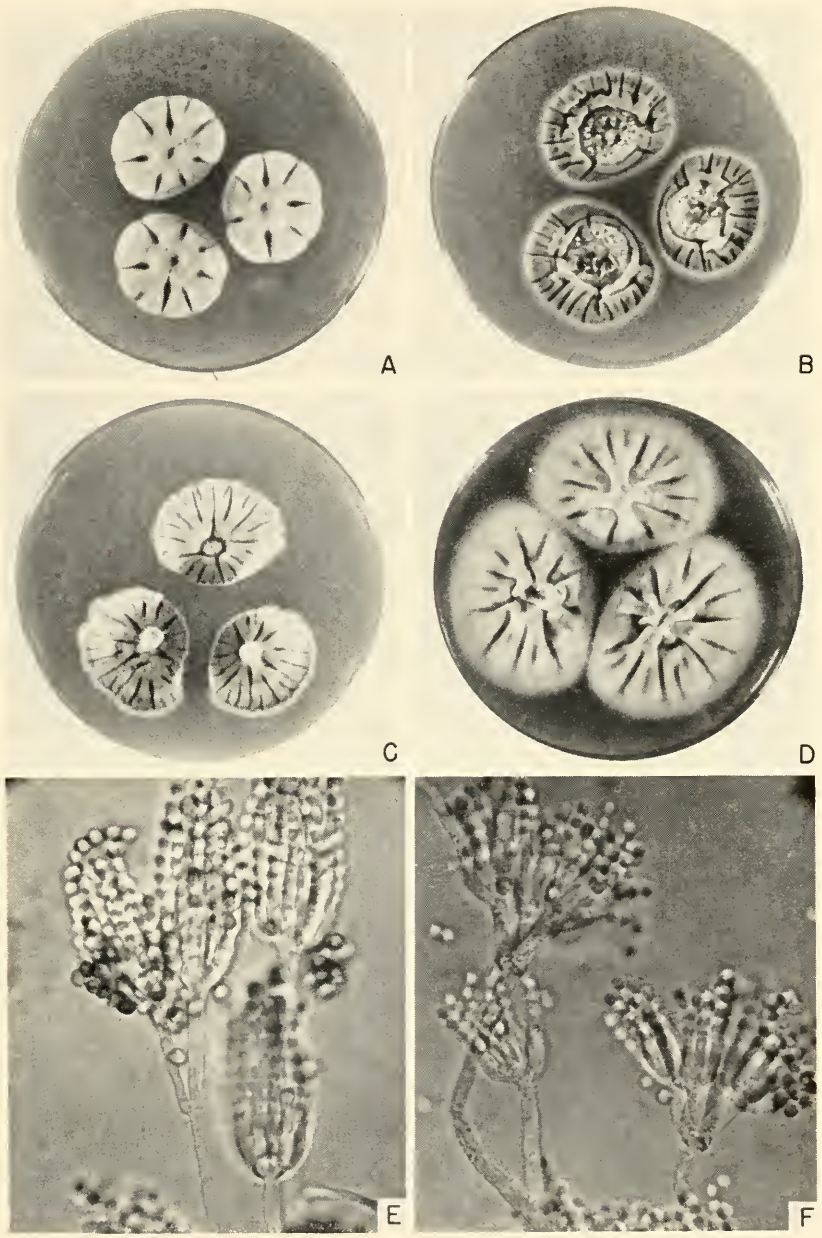


FIG. 68. Members of the Ramigena series. *A*, *Penicillium cyaneum* (Bain. and Sart.) Biourge, NRRL 775, on Czapek agar at two weeks. *B*, *P. waksmani* Zaleski, NRRL 777, on Czapek. *C*, *P. charlesii* Smith, NRRL 1887, on Czapek. *D*, *P. velutinum* v. Beyma, NRRL 2069, on Czapek. *E* and *F*, Detail of penicilli in *P. charlesii* and *P. waksmani*, respectively, × 900.

velvety, with growing margin white, 1.0 to 1.5 mm. wide, otherwise heavily sporing throughout, near dark glaucous gray to grayish blue-green (R., Pl. XLVIII); exudate limited; conidiophores comparatively long, up to 200μ or more in length by 1.5 to 2.0μ, with walls smooth, commonly unbranched or with branches long and limited in number; penicilli consisting of simple, crowded verticils of 8 to 12 parallel sterigmata measuring 10 to 12μ by 1.5 to 2.0μ, approximately uniform in diameter throughout the greater portion of their length but tapering to narrow conidium-bearing tubes; conidia as described above.

Colonies on malt extract agar like the preceding except looser in texture, not furrowed, somewhat deeper, up to 2 mm. in central areas, sporulating abundantly in sub-central to sub-marginal area; color of conidial areas as on steep agar; conidiophores are even longer than on steep agar and the penicilli usually show fewer sterigmata; conidia as described above.

Species description centered upon NRRL 775. This culture was received originally by Thom from the Bainier collection, and was subsequently carried in Thom's collection as No. 4640.422 and used as the basis of his emended description of *Citromyces cyaneus* Bainier and Sartory in his Monograph (1930, pp. 226–228). Thom presented reasons for regarding the culture as type, and the strain still retains the cultural and microscopic characteristics exhibited at that time. Strains approximating this culture are occasionally encountered.

Penicillium waksmani Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 468–469; Taf. 49. 1927. Thom, The Penicillia, pp. 230–231. 1930.

Colonies on Czapek's solution agar growing rather restrictedly, attaining a diameter of 1.5 to 2.0 cm. in ten days at room temperature, strongly wrinkled and buckled, with central area generally raised 1 to 2 mm. (fig. 68B), consisting of a closely-woven basal felt of delicate hyphae, appearing velvety in marginal areas after one week, margin thin and with submerged mycelia usually extending 1 mm. or more beyond the aerial growth, medium to light sporulating after one week, in pale blue-green shades near court gray or celandine green (Ridgway, Pl. XLVII) to deep or dark olive gray (R., Pl. LI) in older colonies; exudate limited in amount, in small droplets, clear; odor lacking or indefinite; reverse uncolored or in pale peach shades; conidiophores arising from the basal felt as ascending, criss-cross rather than erect branches, from very short to 100 to 200μ in length by 1.5 to 2.0μ in diameter, with apices somewhat enlarged up to 2.5 to 3.0μ, smooth-walled or nearly so; penicilli monoverticillate, often appearing singly, sometimes in irregular clusters of 2, 3, or more, borne on separate branches and retaining their individual monoverticillate character

(fig. 68F); sterigmata in compact clusters of 6 to 10, mostly 6 to 8μ by 2.0 to 2.5μ, diverging at the tips; conidia globose to subglobose, mostly 2.0 to 2.5μ, occasionally larger with walls delicately roughened, in divergent chains 50 to 100μ in length, becoming tangled.

Colonies on steep agar growing more rapidly, 2.5 to 3.0 cm. in 10 to 12 days, strongly wrinkled in a radial pattern, commonly appearing definitely angular in outline, consisting of a tough basal felt, bearing abundant conidial structures throughout, velvety, near gnaphalium green becoming mouse gray (R., Pl. LI) in age, growing margin white, narrow, about 1 mm.; exudate lacking or limited, clear; odor lacking or sourish; reverse in dull peach shades; penicilli larger and more consistently branched than on Czapek, commonly appearing as a terminal verticil of three or more branches (metulae); conidiophores slightly heavier, sterigmata and conidia as described above.

Colonies on malt agar growing as on steep agar but less definitely wrinkled and with marginal area plane, velvety, heavily sporing throughout, colored as above; conidiophores arising from submerged or loosely interwoven hyphae, penicilli as described above but more commonly showing branches in a terminal verticil and conidia in longer chains, 100μ or more, tangled.

Species description centered upon NRRL 777 received in 1928 from the Centraalbureau as Zaleski's type and discussed by Thom in his Monograph (1930) as No. 5010.36. Represented in our study by an additional substrain of the same culture received in July 1946, from the Centraalbureau; and by a third culture from the same source diagnosed by them as *Penicillium waksmani* Zaleski. This latter culture had been received by them from the Instituto Sieroterapico, Milan, in 1929 as *P. weidemanni* Westling var. *fuscum* Arnaudi. Strains showing the general cultural and morphological characters of the species are occasionally isolated from soil.

NRRL 781, isolated in 1936 as one of two Penicillia from a culture received from the Centraalbureau in 1936 as "*P. australicum* Hann, Zach", shows the general cultural and morphological characteristics of typical *P. waksmani* strains, but differs from them in the lighter color of its conidial areas, which approximate pale olive buff shades.

Penicillium waksmani resembles rather closely *P. corylophilum* Dierckx (*q.v.*), both in its basic colony appearance and in the general character of its penicilli. Penicilli are, however, more regularly monoverticillate, and conidia are globose and definitely roughened in contrast to the smooth-walled elliptical to subglobose conidia of *P. corylophilum*. The two species should be regarded as closely related, and as possibly forming a bridge between the Monoverticillata and the *P. citrinum* series. *Penicillium waksmani* Zaleski is somewhat arbitrarily assigned to the former

group in the Ramigena series, whereas, *P. corylophilum* is considered as more closely related to *P. citrinum*, hence is placed in that series.

Penicillium charlesii Smith, in Brit. Myc. Soc. Trans. **18:** 90–91, Pl. V, figs. 7 and 8. 1933.

Colonies on Czapek's solution agar growing rather restrictedly, attaining a diameter of 2 cm. in 10 to 12 days, strongly buckled, and wrinkled with central area commonly depressed (fig. 68C), consisting of a comparatively thin, close-textured, tough basal felt, appearing velvety or nearly so, medium to light sporing throughout, heavier in submarginal area, in dull green shades near artemisia or lily green (Ridgway, Pl. XLVII) becoming olive gray in age, with growing margin thin, narrow, rarely exceeding 1 mm., white; exudate lacking; odor slight, nor distinctive; reverse in dull greenish shades; conidiophores arising from creeping or closely interwoven aerial hyphae, simple or variously branched, occasionally showing a fairly compact group of metula-like branches, each branch bearing a monoverticillate penicillus (fig. 68E) with conidial chains forming a compact column up to 150μ or more long, conidiophores variable in length from very short up to 100μ or more by 2.0 to 2.5μ in diameter with terminal area enlarged, occasionally wedge-shaped or more commonly with apices inflated, somewhat vesicular about 4.0 to 5.0μ, walls smooth or nearly so in our cultures (reported as slightly roughened by G. Smith), sterigmata in compact clusters, roughly parallel, numbering up to 10 or 12 in the verticil, 7.5 to 9.0μ by 2.2 to 2.5μ; conidia ovate to slightly elliptical, roughened, mostly 2.5 to 3.0μ by 2.0 to 2.5μ, dark green in mass.

Colonies on steep agar growing more rapidly, 2.5 to 3.0 cm. in 10 to 12 days, strongly and radially wrinkled with central areas variously umbonate or depressed, comparatively thin, close-textured, tough, appearing velvety, heavily sporing throughout in deep blue-green shades approximating lily green (R., Pl. XLVII); no exudate; odor not distinctive; reverse uncolored or in light drab shades; conidiophores as described above but commonly up to 200μ in length; penicilli as described above but more frequently developing from terminal aggregates of metula-like branches and, in individual penicilli, not infrequently showing sterigmata and "metulae" borne from the same node; conidia as described above.

Colonies on malt agar growing restrictedly, about 1.5 cm. in 10 to 12 days, plane or slightly umbonate in central area, velvety, heavily sporing throughout, deep blue-green near lily green, no exudate; no odor; reverse uncolored; conidiophores arising mostly from submerged or ascending aerial hyphae, commonly 200μ or more in length by 2.0 to 2.5 or 3.0μ in diameter with walls often appearing finely granular, loosely branched

with penicilli usually well separated and producing conidia in long narrow columns 100 to 200μ in length; details of penicillus as described above but commonly showing apices more strongly inflated, up to 6 or 8μ; bearing a greater number of sterigmata up to 15 or 18, closely crowded, parallel, tips slightly encurved; conidia as described above.

Species description centered upon NRRL 1887 received from Geo. Smith in August 1942, as type. NRRL 778, received in 1932 from Geo. Smith, as No. P146, an unnamed strain, subsequently used as the type for his *Penicillium charlesii*, differs only in producing colonies less heavily sporulating on Czapek and steep agars. A third substrain of the type, received from the Centraalbureau in February 1946, duplicates NRRL 1887 in essential characteristics but produces less heavily sporulating colonies on Czapek and more closely wrinkled colonies on steep agar. NRRL 780 brought by Dr. Paul Simonart from Biourge's laboratory in 1936 and diagnosed at that time as *P. waksmani* Zaleski likewise represents a strain of *P. charlesii*, differing from the type only in producing slightly faster growing and looser-textured colonies on malt agar.

Strains showing the general cultural characteristics and microscopic details of *Penicillium charlesii* are occasionally isolated from soil and from organic substrata exposed to soil contamination. Such cultures have appeared repeatedly among molds isolated from fabrics such as tentage and other military equipment undergoing deterioration in tropical and subtropical areas. Strain NRRL 2055 is representative of such isolates. In its general appearance in culture, *P. charlesii* Smith like *P. waksmani* Zaleski, appears to occupy a position somewhat transitional between a strictly monoverticillate group and the *P. citrinum* series.

The following species described by Bainier and Sartory are believed to have approximated forms similar to those that we now regard as either *Penicillium waksmani* Zaleski or *P. charlesii* Smith. Due to inadequate colony descriptions (based primarily upon licorice stick cultures) and to the unavailability of authentic cultures for comparative study, it is now believed virtually impossible to recognize these forms or to assign them more exactly to particular species:

C. affinis B. and S., in Bul. Soc. Mycol. France **28**: 39–43; Pl. I, figs. 1–7. 1912.
C. brevis B. and S., in *ibid.* **28**: 43–45; Pl. II, figs. 1–4. 1912.
C. minutus B. and S., in *ibid.* **29**: 137–144; Pl. IV, fig. 3. 1913.
C. musae B. and S., in *ibid.* **29**: 154–157; Pl. V, figs. 1–2. 1913.
C. ramosus B. and S., in *ibid.* **29**: 144–148; Pl. IV, figs. 1–2. 1913.

Conidia were reported to be globose in *Citromyces minutus*, *C. brevis*, *C. ramosus*, and were apparently so in *C. affinis*. *Citromyces musae* was

reported to have conidia elliptical to globose, about 3 by 2μ or globose 2μ in diameter. It is thus possible that the latter more nearly approximated *Penicillium cyaneum* (B. and S.) Biourge. All of the above forms were reported to have an optimum temperature of about 26–28°C., to liquefy gelatine, to peptonize and coagulate milk, and to produce some citric acid from glucose.

Penicillium velutinum van Beyma, in Zentbl. f. Bakt., etc., (II) **91:** 352–353, fig. 6. 1935.

Colonies on Czapek's solution agar fairly rapidly growing, attaining a diameter of 4.5 to 5.0 cm. in 12 to 14 days, consisting of a tough basal felt overlaid by a network of fine aerial hyphae producing an almost floccose effect, central portions raised, about 3.0 to 4.0 mm. deep, remaining almost white, irregularly buckled and wrinkled (fig. 68D), often splitting in the center permitting growth and sporulation to occur on the undersurface of the agar, marginal and submarginal zones somewhat thinner, radially furrowed, light to heavy sporing after two weeks, almost velvety, but showing abundant interlacing hyphae, in blue-green shades near greenish glaucous blue or bluish gray-green (Ridgway, Pl. XLII), becoming slate olive to deep slate olive (R., Pl. XLVII) in age; no exudate produced; odor lacking or indefinite; reverse in vinaceous orange shades from tilleul buff to vinaceous buff or avellaneous (R., Pl. XL) becoming sorghum brown in age (R., Pl. XXXIX); conidiophores commonly borne as branches from aerial hyphae, occasionally directly from the substratum, mostly 50 to 100μ long by 1.5 to 2.0μ in diameter, infrequently much longer, up to 250μ, with walls smooth; penicilli sometimes strictly monoverticillate, usually ramigenous and irregularly branched, ranging from a terminal group of metula-like branches to one, two, or more asymmetrically arranged members, unequal in length, appearing independent and retaining their monoverticillate character, bearing conidial chains up to 100μ in length, usually tangled, sometimes loosely parallel; branches ranging from 5 to 20μ or more by 1.5 to 2.0μ; sterigmata usually in simple verticils numbering 3 or 4 to 8 or 10, occasionally bearing secondary sterigmata, again occurring singly, mostly 6.0 to 8.0μ by 1.5 to 2.0μ, with tips somewhat pointed and usually divergent; conidia globose or nearly so, about 2.5 to 3.0μ, with walls rough, echinulate, appearing dark olive green in mass.

Colonies on steep agar spreading broadly, essentially as on Czapek but with centers usually not as conspicuously raised, rather closely furrowed in a radial pattern, broadly zonate, growing margin broad, white, almost cottony, 4.0 to 5.0 mm., otherwise medium sporing throughout, in dull gray-green shades near gnaphalium green (R., Pl. XLVII), becoming dull

in age, reverse in vinaceous shades to sorghum or Hay's brown (R., Pl. XXXIX); penicilli as described above.

Colonies on malt spreading as on steep agar, loose-textured, appearing almost floccose, not furrowed, light sporing with conidial heads colored as above; reverse in golden brown shades; conidial structures as described above but with conidiophores often finely roughened.

Species description centered upon van Beyma's type received from the Centraalbureau in July 1946, and since entered in our Collection as NRRL 2069. The type strain was isolated from sputum in 1932. Other cultures representative of the species have not been reported although the original isolate may have represented only a dust-borne inhalant.

This species is placed in the ramigenous series upon the basis of its penicilli. Close relationship to other members of the series is not claimed. In contrast to other species assigned here, which are slow growing, this species is characterized by its very rapidly and broadly spreading colonies. In general texture and appearance, and in the manner in which the conidial structures are borne, the species is strongly suggestive of *Penicillium spinulosum* Thom, and may represent only a variant form in which the penicilli are usually branched. This possible relationship is further suggested by the rough, echinulate character of its conidia, and by the development of vinaceous to dull brownish purple shades in colony reverse.

Occurrence and Significance

Members of the Ramigena series regularly occur in soil, and may be isolated also from a variety of organic substrates undergoing slow decomposition in the field. They were encountered quite frequently among the molds isolated from fabrics, optical instruments, and other items of military equipment undergoing deterioration under service conditions in tropical and subtropical areas. One species, *Penicillium capsulatum*, described as new by Raper and Fennell (1948), was repeatedly encountered from this source, hence is believed to be widely distributed in the soils of warmer areas. *Penicillium waksmani* Zal. and *P. charlesii* Smith, were likewise encountered among molds isolated from deteriorating materiel. *Penicillium velutinum* v. Beyma (1935), originally from sputum, probably represented an air-borne saprophyte.

Penicillium waksmani was reported by Hubert (1938) to be capable of growing in saturated solutions of $CuSO_4$, and in 15 percent solutions of ethyl alcohol. Formaldehyde at 0.2 percent, killed the spores. Otomo (1935) found *P. waksmani* to be common on moldy soybean cakes. This organism, together with a limited number of other species, mostly members of the *Aspergillus glaucus* group, reduced the amount of fat, carbohydrates,

and water but did not alter the nitrogen content. Moldy soybean cake was reported to have a favorable effect upon rats when added to their ration.

The biochemistry of *Penicillium charlesii* has been studied quite extensively, particularly by Professor Raistrick and co-workers in England. The type strain of this species was isolated by J. H. V. Charles from moldy Italian maize, and was recognized to possess unique biochemical reactions when described by George Smith in 1933. Clutterbuck, *et al.* (1934), found six new optically active acids to be produced by this mold when grown upon Czapek-Dox or Raulin-Thom solutions containing glucose as a carbon source. These were shown to have the following empirical formulae, and for them the accompanying names were proposed: $C_9H_{10}O_4$, carolic acid; $C_9H_{12}O_7$ ($C_9H_{10}O_6 \cdot H_2O$) carolinic acid; $C_{10}H_{10}O_6$, carlic acid; $C_{10}H_{12}O_6$, carlosic acid; $C_{16}H_{20}O_6$, ramigenic acid; and $C_{26}H_{32}O_{12}$, verticillic acid. Carolic acid, produced in the greatest yields, is monobasic and dextrorotatory, M.P. 123°C. Carlic acid, produced in small amounts, is dibasic and laevorotatory, M.P. 176°C. Carlosic acid, produced in moderate yields on Czapek-Dox medium only, is dibasic and laevorotatory, M.P. 181°C. Ramigenic acid, produced in small amounts on both media, is dextrorotatory, M.P. 171°C. but softens at 125°C. Verticillic acid, produced in large yields on Raulin-Thom medium, is tetrabasic and laevorotatory, M.P. 171°C. In addition to these acids, *P. charlesii* produced two new polysaccharides, a polygalactose and a polymannose which, upon hydrolysis, yielded *d*-galactose and *d*-mannose. Both polysaccharides were produced on both media in considerable amounts, and afford examples of the ready conversion of glucose into galactose and mannose by a mold. The molecular constitutions of carolic and carolinic acid was carefully investigated by Clutterbuck, Raistrick, and Reuter (1935a) and were shown to be closely related derivatives of *l*-γ-methyltetronic acid, and closely related structurally to ascorbic acid (Vitamin C). In another paper (1935b) these authors reported molecular constitution of carlic and carlosic acid. These acids were shown to be closely related derivatives of *l*-γ-carboxymethyltetronic acid and to be structurally closely related to carolic and carolinic acid and to ascorbic acid. In a third paper (1935c) the formation of *l*-γ-methyltetronic acid ($C_5H_6O_3$) was described, and ramigenic and verticillic acids, previously reported, were shown to be artefacts arising from the condensation of *l*-γ-methyltetronic acid and acetone.

Herbert and Hirst (1935) found the absorption spectra of carolic, carolinic, carlic, and carlosic acids to be strikingly similar to that of ascorbic acid, to which they are closely related in structure. The presence of these

acids in samples of ascorbic acid leads to serious errors when the latter is assayed by spectrophotometric method.

Haworth, Raistrick and Stacy have published related studies on the polysaccharides produced from glucose by *Penicillium charlesii*. In the first of these (1935a), the molecular structure of mannocarolose was reported, and upon acid hydrolysis, *d*-mannose was produced as the sole hydrolytic product. In the second (1937), the molecular structure of galactocarolose was reported and *d*-galactose represented the sole product upon mild acid hydrolysis.

Chapter VIII

ASYMMETRICA

Included in this section are all of the Penicillia which produce conidial structures consisting of two or more series of cellular elements (i.e., sterigmata, metulae, and branches), and in which the branching system is typically irregular, one-sided, or asymmetrical. The elements comprising such penicilli develop ordinarily in basipetal succession, i.e., the first group of sterigmata develop upon the tip of the main axis, then a verticil of metulae develops from the next lower node or septum, and branches, when present, arise successively lower down on the conidiophore. Since these branching elements are, as a rule, incompletely verticillate, the penicillus appears more or less one-sided, or asymmetrical, in arrangement.

The general type of penicillus described is an arbitrary common character that brings together several more or less well-defined groups, which we consider as Sub-sections. Each of the sub-sections embraces two or more series which, for the most part, are believed to represent natural groupings of species and strains. They are differentiated upon the general pattern of the penicillus and the character of the aerial growth, with particular reference to the origin and arrangement of the conidiophores. Five sub-sections are recognized as follows:

Divaricata, characterized by strongly divaricate penicilli, often presenting the overall aspect of an irregular and terminal cluster of monoverticillate structures.

Velutina, usually producing penicilli that are once- or twice-branched below the level of the metulae, and characterized particularly by the development of abundant conidiophores in a dense stand from the substratum or a basal felt to produce a conidial layer that is velvety in appearance.

Lanata, producing penicilli much like the preceding, but characteristically developing a loose-textured or floccose aerial mycelium, and producing conidiophores largely from this aerial growth.

Funiculosa, producing penicilli of the same general pattern as above, but with the aerial growth commonly showing a definite to conspicuous ropiness, and with conidiophores commonly arising from such ropes or funicles.

Fasciculata, producing penicilli much like the preceding, but with conidiophores arising almost exclusively from a submerged mycelium and characteristically aggregated into tufts, fascicles, or coremia.

More detailed characterizations of the different sub-sections are given in the introductory statements which precede consideration of the series and species which comprise them.

ASYMMETRICA

Sub-section: DIVARICATA

Penicilli are strongly divaricate in most species, and in the majority of forms consist of a terminal group of irregularly arranged branches and/or metulae bearing clusters of sterigmata (fig. 69). These branches are commonly unicellular and together with the sterigmata borne thereon, present the general appearance of a group of monoverticillate penicilli. The terminal cluster commonly consists of a prolongation of the main axis, or an indefinite number of fertile branches arising irregularly at lower levels to comprise a loosely arranged biverticillate and asymmetric penicillus. In a limited number of species the fertile branches arise at one general level in the manner of true metulae and comprise fairly compact but definitely divaricate penicilli. Colonies often consist of a rather close-textured and comparatively tough basal felt at or near the agar surface, from which a loose-textured and often flocculent overgrowth commonly develops. Most, but not all, species grow rapidly to produce broadly spreading colonies. Vegetative hyphae are generally thin, delicate, and rarely exceed 3.0μ in diameter. Conidiophores may develop directly from the basal felt or arise as branches from aerial hyphae. Walls may be smooth, finely granular, or in a few forms conspicuously roughened.

Members of the group are always present in cultures made from soil, but may occur also upon vegetable remains and upon other organic materials in the later stages of decomposition. They frequently occur on fabrics and other military equipment undergoing deterioration in the field. Some forms are unusually tolerant of and may occur in strong acid solution and in copper and nickel electroplating baths. Others sometimes occur as "bottle imps" in various laboratory reagents.

The Divaricata are regarded as representing, in the main, a natural group of Penicillia. However, the group should be considered as occupying a somewhat intermediate position in the genus as a whole, since different members assigned here show obvious affinities to other well marked groups.

Members of the *Carpenteles* (ascosporic) series show a definite relationship to the *Penicillium javanicum* series of the Monoverticillata (see p. 132), but are excluded from the latter by the consistent development of branched penicilli. Similarly, members of the *P. raistrickii* series seem to be closely related to *P. thomii* and allied species but are separated from them upon the same basis.

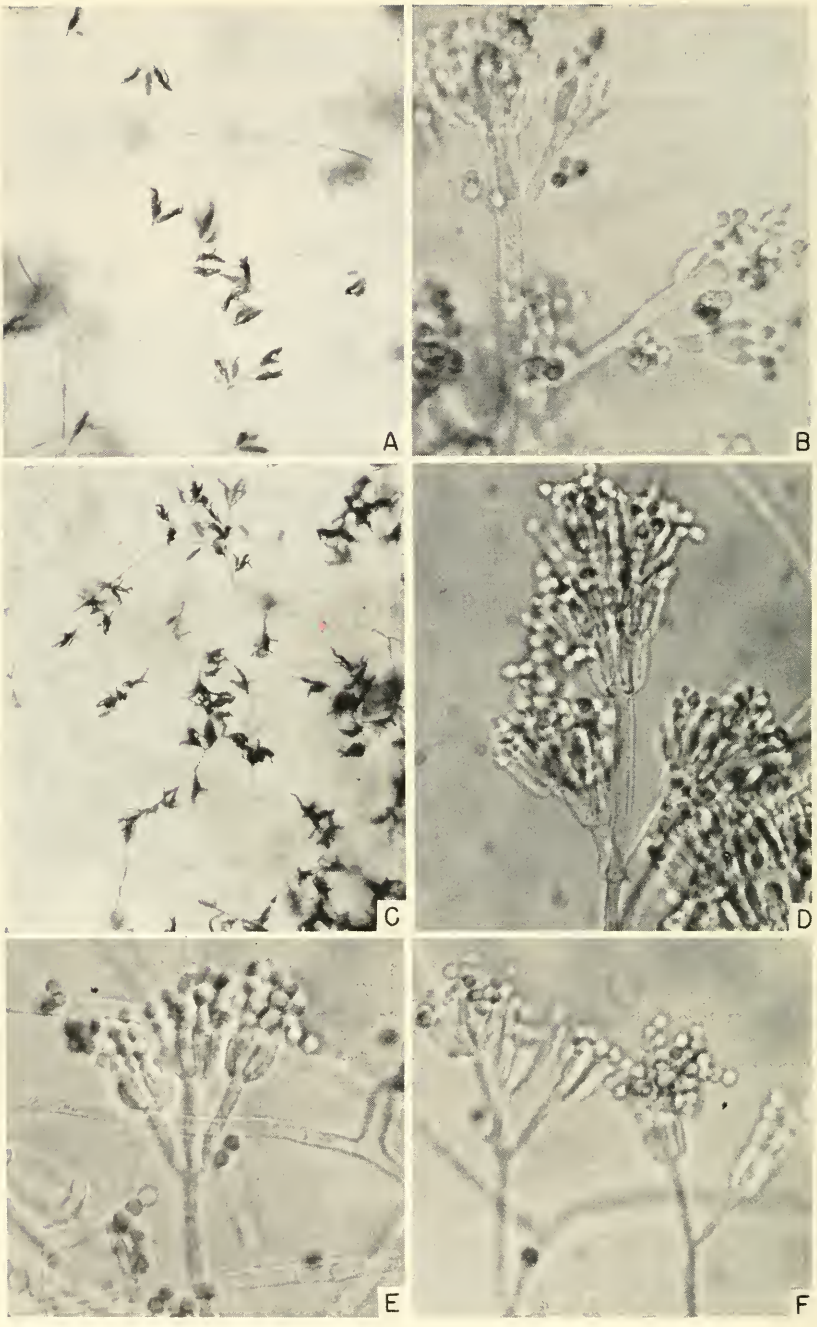


FIG. 69. Penicilli in different members of the Divaricata. *A*, *Penicillium nigricans* (Bain.) Thom, NRRL 915; penicilli as developed along intercolony margin, × 95. *B*, Detail of penicillus in the same strain, × 1000. *C*, *P. lilacinum* Thom, NRRL 2014; penicilli as developed at colony margin, × 85. *D*, Enlarged view of penicillus in the same strain, × 1000. *E* and *F*, Penicilli of *P. janthinellum* Biourge, NRRL 2016, and *P. jensenî* Zaleski, NRRL 909, respectively; × 1000.

Penicillium lilacinum Thom is clearly different from other members of the Divaricata but can, nevertheless, be more satisfactorily included here than elsewhere.

Penicillium nalgiovensis Laxa is tentatively assigned to the Divaricata since we believe that it can be keyed here more easily than elsewhere, but in the loose, deep character of its colonies and in the comparatively large dimension of conidia and cellular parts of its penicilli it is strongly suggestive of the Lanata Section.

Penicillium melinii Thom shows many if not an actual majority of penicilli as truly monoverticillate, but in its general habit, coloration, and cultural characteristics seems to belong with *P. nigricans* (Bainier) Thom which unmistakably belongs in the Divaricata.

Penicillium jenseni Zaleski shows a definite resemblance to some of the ramigenous monoverticillate species but produces sufficient well developed biverticillate penicilli to warrant placement here.

Penicillium soppi Zaleski with verticils of metulae, mostly terminal, is clearly suggestive of the *P. citrinum* series but differs from the latter in the production of small sclerotium-like masses, and in its failure to develop yellow colors or closely compacted columns of conidia.

Penicillium godlewskii Zaleski is included here because of the general character of its conidial structures. Colonies are, however, often markedly funiculose and difficulties sometimes arise regarding the correct placement of individual strains.

Key to the Divaricata

Page

I. Colonies producing perithecia, sclerotia, or masses of thick-walled cells.
  A. Colonies producing true perithecia, at first parenchymatous throughout, then usually sclerotioid, often ripening late..... *Carpenteles* series 260
    1. Ascospores lenticular, 2.5 to 3.0μ in long axis, with equatorial furrow prominent and walls roughened. Perithecia light gray to grayish black (when wet), usually ripening in 5 to 6 weeks *P. asperum* (Shear) n. comb. 263
    2. Ascospores lenticular, 5.0 to 6.0μ in long axis, equatorial ridges parallel and often closely appressed, with walls rough. Perithecia buff to light tan, commonly ripening in 3 to 4 weeks. *P. baarnense* v. Beyma 266
    3. Ascospores lenticular, 2.8 to 3.3μ in long axis, with equatorial area broad, flattened and usually showing two low, widely separated ridges, with walls smooth. Perithecia in cream to light tan shades, usually ripening in 2 to 3 weeks..... *P. egyptiacum* v. Beyma 269
  B. Colonies producing sclerotia or masses of thick-walled cells, but apparently not developing asci and ascospores at any stage.
    1. Conidial areas velvety or nearly so upon most substrata, conidiophores arising from the substratum or from aerial hyphae.
      a. Conidiophore walls coarsely roughened, sclerotia well organized, firm or stony..... *P. raistrickii* series 273

1′. Sclerotia very hard, stony, white to light pink in color, vegetative mycelium white ..... *P. raistrickii* Smith 275

2′. Sclerotia fairly firm, not sclerotioid, yellow to light brown in color, vegetative mycelium often developing yellow shades from encrustment with yellow granules *P. pulvillorum* Turfitt 277

b. Conidiophore walls finely roughened, true sclerotia lacking but small rounded masses of thick-walled cells evident upon all substrata and particularly upon malt agar ..... *P. soppi* Zaleski 279

c. Conidiophore walls smooth or nearly so.

1′. White to pink sclerotia reported ..... *P. rolfsii* Thom 282

2′. Small masses of heavy-walled cells (as in *P. soppi*) produced in some strains ..... *P. miczynskii* Zaleski (see *P. janthinellum* series)

2. Conidial areas commonly showing fasciculation, with conidiophores aggregated into more or less well defined bundles or tufts The Fasciculata (in part) 467

a. Sclerotia abundantly produced, often characterizing the colony at temperatures above 20°C. ..... *P. gladioli* Machacek (see p. 471)

b. Sclerotia reported but seldom produced abundantly *P. italicum* Wehmer (see p. 526)

II. Colonies not producing perithecia, sclerotia, or masses of thick-walled cells.

A. Colonies not showing green, gray-green or blue-green with the ripening of conidia.

1. Colonies deeply floccose, becoming lilac, vinaceous or violaceous with the development of conidia ..... *P. lilacinum* series 284

a. Colonies developing lilacinus (Saccardo) or vinaceous (Ridgway) shades, with reverse similarly colored, or in some strains becoming purple-red ..... *P. lilacinum* Thom 285

b. Colonies developing violet shades near "light lobelia violet" (Ridgway) with ripening of conidia, and with reverse in bright yellow shades ..... *Spicaria violacea* Abbott 288

2. Colonies not deeply floccose, comparatively thin, often strongly wrinkled, becoming pinkish-buff to avellaneous with ripening of conidia. *P. humuli* van Beyma 291

3. Colonies velvety or nearly so, with conidial areas in tan, cream, or near-white shades, never showing green Natural mutants of many species

B. Colonies showing some shade of green, gray, gray-green, or blue-green with the ripening of conidia.

1. Penicilli with divaricate character well marked, sterigmata-bearing branchlets (metulae) scattered on the conidiophore, or commonly only partly aggregated into true verticils.

a. Ripe conidia typically in pale blue-green or gray-green shades and colony reverse often highly colored.

1′. Conidial chains strongly divergent and/or becoming tangled in age, not tending to form columns.

aa. Sterigmata abruptly tapered to narrow conidium-bearing tubes; colonies usually not funiculose *P. janthinellum* series 294

1″. Conidia elliptical, rough with echinulations arranged in spiral or transverse bands.... .....*P. daleae* Zaleski 296

2″. Conidia elliptical to subglobose, usually roughened but with echinulations not arranged in spiral or transverse bands.

aaa. Vegetative mycelium and colony reverse often strongly colored (orange-red, reddish purple, etc.) in new isolates... *P. janthinellum* Biourge 299

bbb. Vegetative mycelium uncolored or light buff to peach; colonies sporulating sparingly or tardily; colony reverse colorless or in yellow to orange shades.

1‴. Conidiophores conspicuously roughened; penicilli commonly consisting of a terminal verticil of divergent metulae; conidia elliptical to subglobose, finely echinulate; reverse uncolored to yellow *P. simplicissimum* (Oud.) Thom 304

2‴. Conidiophores finely roughened; penicilli irregular; conidia elliptical, smooth or finely roughened; reverse in orange shades *P. ochro-chloron* Biourge 305

3‴. Conidiophores smooth or nearly so; penicilli commonly irregular; conidia mostly subglobose, conspicuously roughened; reverse in cream to light tan shades *P. piscarium* Westling 308

4‴. Conidiophores smooth or nearly so; penicilli irregular; conidia subglobose to elliptical, smooth; reverse in bright yellow to yellow-orange shades..... *P. miczynskii* Zaleski 309

bb. Sterigmata not abruptly tapered to conidium-bearing tubes; colonies commonly becoming funiculose *P. godlewskii* Zaleski 312

2′. Conidial chains tending to form columns, at least in young cultures; conidia globose to subglobose, somewhat roughened *P. canescens* series 315

aa. Colony reverse developing deep red or brown shades; penicilli strongly divaricate, not tending toward ramigenous.

1″. Colonies 500 to 1000μ deep, with surface growth loose, more or less floccose; conidial areas in dull blue-green shades; conidia about 2.0 to 2.5μ; reverse orange, becoming rich brown in age... ..... *P. canescens* Sopp 316

2″. Colonies deeply floccose, 2 to 3 mm. deep; conidial areas in brighter greenish glaucous shades; conidia about 3.2 to 3.6μ; reverse in deep red shades near maroon *P. nalgiovensis* Laxa 319

bb. Colony reverse uncolored or in dull peach shades, not developing dark colors; penicilli often appearing somewhat ramigenous.....*P. jenseni* Zaleski 322

b. Ripe conidia typically in dull gray shades (scarcely showing any green) such as steel gray to dark olive gray (Ridgway), globose; colony reverse usually in yellow to deep orange shades
P. nigricans series 323

1′. Conidiophore walls smooth or nearly so on all substrata.
aa. Conidia strongly echinulate with conspicuous color bars.
1″. Colonies heavily sporing, dull to dark gray in color
P. nigricans (Bainier) Thom 325
2″. Colonies floccose, light sporing, white or nearly so
P. albidum Sopp 329
bb. Conidia delicately echinulate.....*P. kapuscinskii* Zaleski 330
2′. Conidiophore walls coarsely roughened, at least on malt agar.
aa. Conidia conspicuously echinulate.....*P. melinii* Thom 331
bb. Conidia smooth or nearly so.....*P. raciborskii* Zaleski 333

2. Penicilli with divaricate character evident, but tending toward compactly biverticillate with metulae usually borne at a single level and conidia producing compact columns that are typically divergent
P. citrinum series
(see The Velutina)

Carpenteles Series

Outstanding Characters

Perithecia characteristically produced, at first parenchymatous throughout, often becoming sclerotioid, ripening from the center outward and often late, in some species and strains not developing asci and ascospore for 4 to 6 weeks or more, with some structures apparently remaining sclerotioid indefinitely.

Asci borne in chains or singly as branches from ascogenous hyphae, 8-spored; ascospores lenticular, with convex walls smooth to conspicuously roughened, showing equatorial areas well marked, with definite furrows and ridges usually apparent.

Colonies of most strains growing fairly rapidly upon most substrata but often restricted on Czapek, characteristically developing abundant perithecia adjacent to the substratum with surface commonly appearing granular, perithecia sometimes massed and characterizing the colony; conidial structures usually limited in number and generally not affecting the colony appearance.

Penicilli typically biverticillate and asymmetric but with monoverticillate structures regularly present in limited numbers, sparsely produced in some strains, more abundantly in others, usually borne on comparatively long, smooth-walled conidiophores arising mostly from the substratum.

Series Key

(See General Key to Divaricata)

The so-called *Carpenteles* series embraces a limited number of ascosporic Penicillia of somewhat uncertain relationship, but of considerable interest

from an historic point of view. Brefeld in 1874 published a detailed account of perithecium formation and ascospore development in a green *Penicillium* which he reported as *Penicillium glaucum* Link. For sixty years his work was neither confirmed nor denied, in spite of diligent search in every culture laboratory in the world. It is now quite impossible to establish with certainty whether or not Brefeld's study was based upon a single species of *Penicillium*. The pattern of the penicilli shown in some of his figures (e.g. fig. 8, Taf. II, reproduced as fig. 2B in this Manual) indicates larger and more complex structures (possibly approximating *P. expansum* Link, or some other fasciculate form) than those usually seen in the present series. Nevertheless, the development of the perithecium as reported and illustrated by him suggests some member of the *Carpenteles* series.

Langeron (1922) proposed the generic name *Carpenteles* for species of *Penicillium* which were known to produce asci, and specified as the type of his new genus "*P. glaucum* (Link) Brefeld". Langeron based his new genus upon bibliographic considerations only, and did not see the fungus nor verify the connection between the conidia and perithecia described by Brefeld. His usage was not accepted by Thom (1930) for lack of valid work relating the name to actual material.

Shear, in 1934, examining soil isolates from Honduras sent to him by Dr. Reinking, encountered a culture which he believed to represent Brefeld's *Penicillium*, but rejected the name *P. glaucum* because of "the confusion which already exists in its use". He then proposed the name *Carpenteles asperum* nom. nov., with the specific name referring to the spinulose ascospores. Shear was amply justified in proposing a new specific name for the very reasons which he gave. There was no justification, however, for resurrecting a generic usage which was originally ill-conceived and which subsequently had been properly ignored.

There is some good evidence in support of Shear's view that his *Carpenteles asperum* approximated Brefeld's fungus. The perithecia are sclerotoid in the extreme, mature very late, and ripen from the center outward as reported by Brefeld. Furthermore, the ascospores are definitely ridged and conspicuously roughened and agree closely with Brefeld's figures (45 and 46, Taf. VII) reproduced as fig. 2G in this Manual. Mycelia originating from these rough ascospores were figured as developing biverticillate-asymmetric penicilli often closely approximating in pattern those now produced by Shear's type. Further than this, one cannot go. Shear gave no cultural descriptions, and he discussed morphological details only in the briefest manner. Fortunately we still have his cultures, and one of these (NRRL 715) has retained its original cultural characteristics; otherwise, we would have no certain proof of the fungus with which he worked.

Emmons, in his study of the ascocarps of species of *Penicillium* (1935), suggested that *Penicillium egyptiacum* van Beyma (1933) more nearly approximates Brefeld's *P. glaucum*. This belief was based primarily upon the disposition of asci in chains, a development which Brefeld clearly illustrated and one which seldom, if ever, occurs in the fungus studied by Shear. Emmons' report that the asci in Shear's species are borne singly as short branches from fertile ascogenous hyphae has been confirmed in our present study.

In our experience, van Beyma's *Penicillium baarnense* (1939/40) might better represent the fungus studied by Brefeld. In this species the asci are borne in chains, ascospores are rough-walled, and perithecia are for a time strongly sclerotioid and ripen comparatively late. Furthermore, the dimensions of its ascospores more nearly approximate the measurements given by Brefeld than do those of either *P. asperum* or *P. egyptiacum*.

Any one, or none, of the species now assigned to the *Carpenteles* series may actually represent Brefeld's *Penicillium glaucum*. It is possible, as a matter of fact, that there exists still another species, probably in this general series, which may show all of the characteristics of his fungus, including the large rebranched penicilli which commonly have been assumed to belong to a different species. Such a *Penicillium*, however, has not yet been rediscovered.

In the present work we have adopted the designation Carpenteles series to cover the species under consideration because of the recurrence of this generic name in recent literature, and in the belief that it can be used advantageously to include the ascosporic Penicillia that produce asymmetrical conidial structures, usually biverticillate, in conjunction with perithecia that are initially parenchymatous throughout and which commonly become sclerotioid prior to maturation. Our Carpenteles series contains three well defined species, namely: *Penicillium asperum* (Shear) n. comb., *P. baarnense* van Beyma, and *P. egyptiacum* van Beyma. These species may be separated in the manner shown in the general key to the Divaricata (see p. 257), and may be briefly characterized as follows: *P. asperum* typically produces abundant sclerotioid perithecia dull gray to silver gray in color upon most substrata; asci and ascospores develop very late and often in limited numbers; and ascospores show prominent equatorial furrows and ridges with side-walls conspicuously roughened. *Penicillium baarnense* typically produces sclerotioid perithecia in buff to light tan shades; asci and ascospores develop late; and ascospores are comparatively large, show prominent, often closely parallel equatorial ridges and rough side-walls. *Penicillium egyptiacum* regularly produces abundant pseudoparenchymatous perithecia in cream to light tan shades; asci and ascospores usually develop in 2 to 3 weeks; and ascospores show broad equa-

torial areas marked by two low, widely separated ridges and smooth sidewalls. Each of these species produce penicilli usually consisting of a terminal cluster of 3 to 4, often divergent, metulae. Monoverticillate structures occur in considerable numbers in all cases.

The above species seem to bear a definite relationship to *Penicillium javanicum* and allied species and it is possible that the two series should be considered together as comprising a single natural group. This is indicated by a striking resemblance in the appearance and in the developmental history of the perithecia in the two series. While we have made no detailed histological study of perithecium formation in these forms, our observations of plate cultures on many different substrata confirm Emmons' report (1935) that the perithecia of *P. asperum* and *P. egyptiacum* originate and develop in the same manner as described by Dodge (1933) for *P. brefeldianum* (see p. 133). Close relationship is further indicated by the frequent, though possibly atypical, development of biverticillate penicilli in some members of the monoverticillate *P. javanicum* series, and by the frequent occurrence of monoverticillate structures in the biverticillate Carpenteles series. As a matter of convenience, we have separated ascosporic species with definite walled perithecia into two series upon the type of penicillus usually produced, but this treatment may prove too arbitrary. Only by the isolation and examination in culture of additional members of both series, as they are now constituted, can the true relationships of these ascosporic forms be established.

Members of the *Carpenteles* series likewise bear a striking resemblance to *Penicillium raistrickii* and allied sclerotial forms in the general pattern of their penicilli. In fact, they differ from the latter primarily in the formation of asci and ascospores, a development which commonly occurs late and not infrequently fails of completion. There is little morphological difference to distinguish a typical strain of *P. raistrickii* from a strain of *P. asperum* that fails to develop ascospores, except the coarsely roughened conidiophores of the former species.

Penicillium asperum (Shear) n. comb.

Synonym: *Carpenteles asperum* Shear, in Mycologia **26:** 104–107, figs. 1–3. 1934; also Emmons, in Mycologia **27:** 146, figs. 15 and 16. 1935.

Colonies on Czapek's solution agar rather slow growing, attaining a diameter of 2.5 to 3.0 cm. in 10 to 12 days at room temperature, in age almost covering the culture plate, strongly wrinkled and buckled at least in central area, comparatively thin, consisting of a tough, fairly brittle basal felt, with surface growth thin and fibrous, usually producing very few conidial structures within one to two weeks or longer; at first white,

in some strains remaining so, in others becoming light gray in 6 to 10 days from the development of abundant sclerotioid perithecia (fig. 70A), in still other strains (mostly long maintained in culture) developing peni-

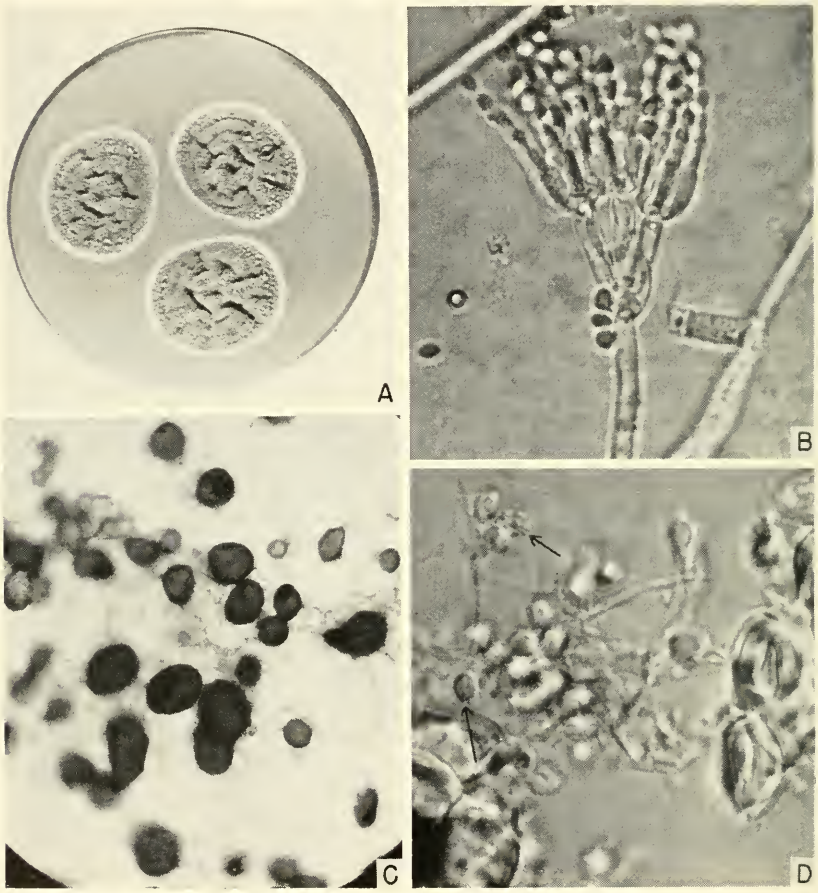


FIG. 70. *Penicillium asperum* (Shear) n. comb. *A*, Two-week old colonies of strain NRRL 2088 on Czapek agar. *B*, Penicillus as developed in strain NRRL 715, × 1300. *C*, Low-power view of perithecia in NRRL 715 on corn meal agar, × 40. *D*, Ascospores from the same, × 1500; note furrowed ascospores marked by arrows and the thick-walled cells (right and lower left) that comprise much of the sclerotioid perithecium.

cilli rather abundantly in marginal areas which appear velvety and show gray shades near court or mineral gray (Ridgway, Pl. XLVII); exudate fairly abundant, clear, in small droplets; odor lacking or indefinite; reverse at first colorless, in age becoming dark brownish to fuscous in central

areas; conidial structures ranging from few to abundant in different strains; conidiophores arising primarily from the substratum, but sometimes from aerial hyphae, up to 500μ or more in length by 2.2 to 2.8μ in diameter, with walls smooth but often appearing granular to vacuolate within, bearing biverticillate asymmetric penicilli (fig. 70B) which are often strongly divaricate; penicilli irregular in pattern, commonly consisting of a terminal verticil of 3 or 4 divergent metulae and often showing one or more metulae arising below the level of the verticil, mostly 10 to 15μ by 2.2 to 2.8μ; sterigmata in compact verticils of 5 to 8, mostly 8 to 10μ by 2.0 to 2.2μ, with conidium-bearing tubes definitely narrowed; conidia elliptical, mostly 2.2 to 3.0μ by 2.0 to 2.5μ, smooth-walled; perithecia abundantly produced in most strains but commonly diminishing with long cultivation, often massed and characterizing the colony, sometimes scattered and obscured by overlying vegetative hyphae, variable in form and dimensions, spherical, oblong to elongate or somewhat angular (fig. 70C), up to 400 to 500μ in diameter, extremely hard, crushing with difficulty, composed of heavy-walled parenchyma-like cells, at first uniform in structure throughout, ripening late from the center outward, with asci and ascospores usually not appearing for 5 to 6 weeks or longer, and in some cases apparently never developing ascospores; asci spherical to oval about 5.5 to 6.5μ in diameter, apparently borne singly on lateral branches from a network of fertile hyphae which fills the central area of the ripening perithecium; ascospores lenticular, about 2.5 to 3.0μ by 2.0 to 2.2μ with convex surfaces more or less roughened, and with two often closely appressed equatorial ridges about 0.5μ wide (fig. 70D).

Colonies on steep agar growing more rapidly than on Czapek, approximately 4.0 to 4.5 cm. in 10 to 12 days at room temperature, with growing margin white, 1 to 2 mm. wide, strongly furrowed in a predominantly radial pattern, in general texture and appearance as on Czapek but developing perithecia more abundantly and more rapidly, usually in silver gray shades from massed perithecia (Col. Pl. V), producing very few penicilli; perithecia as described above in form, dimensions and development.

Colonies on malt agar about 3.5 to 4.0 cm. wide in 10 to 12 days, thin, consisting of a dense layer of perithecia at the agar surface, overgrown in central colony areas by a loose network of aerial hyphae up to 1 to 2 mm. deep, approximately pallid quaker drab to pallid mouse gray (Ridgway, Pl. LI), darkening slightly in age, becoming vinaceous buff to avellaneous (R., Pl. XL); penicilli few in number and not affecting the colony appearance; perithecia as described above but commonly developing ripe ascospores in 4 to 5 weeks.

Species description based upon NRRL 715 which was received in 1931 from Dr. C. L. Shear as a culture from Dr. Otto A. Reinking, isolated

originally from soil at Tela, Honduras. This culture was subsequently cited by Shear (1934) as one of the types for his *Carpenteles asperum*. The species is also represented by additional strains as follows: NRRL 2088, isolated in October 1945, from a sample of soil sent to us from Cocoa River, Nicaragua, by Dr. A. G. Kevorkian; NRRL 2089, isolated in December 1945, from a sample of soil sent to us by Dr. O. G. Lima, Recife, Brazil; and NRRL 714, received originally from Shear as his No. R2, one of the type strains of his *Carpenteles asperum*. This last strain has almost completely lost the capacity to produce sclerotioid masses (perithecia?) during the fifteen years that we have maintained it in artificial culture, but conidial structures of the type described above are abundantly produced. We can assume that the original strongly perithecial strain has been supplanted by a variant that is predominantly conidial.

In *Penicillium asperum* the sclerotioid masses which subsequently develop as perithecia are unusually hard. They ripen late in all strains, and during the first three or four weeks, closely resemble the true sclerotia of such forms as *P. thomii* Maire and *P. raistrickii* Smith in general texture and firmness. In some strains and upon certain media, asci and ascospores may appear within four weeks. Upon other media, ripening of the perithecia in the same strains may be much delayed. Different strains also vary in regard to ascospore development. No asci or ascospores have been observed after intervals up to three months in one culture appearing otherwise typical. The process of maturation is essentially like that described by Dodge (1933) for *P. brefeldianum*. Ripening is from the center outward and an expanding core of fertile hyphae seems to gradually digest the sclerotioid mass. When this process has progressed throughout approximately half the diameter of the body, asci usually begin to appear. Unlike those of *P. baarnense* and *P. egyptiacum*, these are apparently borne singly on short lateral branches. The asci are 8-spored and the ascospores apparently develop in the usual manner. There is evidence of the development of a fertile, hyphal network, or "skein", as reported by van Beyma in the description of *P. javanicum* (1929), but this is not so pronounced as in some species such as *P. baarnense*.

Penicillium baarnense van Beyma, in Antonie van Leeuwenhoek **6:** 270–273, figs. 5 and 6. 1939/1940.

Synonym: *Penicillium* (*Carpenteles*) *baarnense* van Beyma, *ibid.*

Colonies on Czapek's solution agar growing rather restrictedly, attaining a diameter of 2.5 to 3.0 cm. in 12 to 14 days at room temperature, comparatively thin, with central area more or less wrinkled and furrowed and outer zone 2 to 3 mm. wide, plane (fig. 71A), surface appearing slightly flocculent, at first white but developing light buff shades in about 2 weeks

with the appearance of perithecia, conidial structures limited in number, not affecting the colony appearance, perithecia abundantly produced throughout the whole colony or in localized V-shaped sectors; exudate clear, abundantly produced in central colony areas; odor lacking or indistinct; reverse uncolored to light golden tan in age; conidiophores arising mostly from the substratum, sometimes from aerial hyphae, from 50 to

FIG. 71. *Penicillium baarnense* v. Beyma, NRRL 2086. *A* and *B*, Two-week-old colonies on Czapek and malt agars. *C*, Low-power view of perithecia, × 40. *D*, Ascospores showing characteristic furrow and rough walls, × 1500.

300μ, mostly 100 to 200μ by 2.2 to 3.0μ, with walls smooth; penicilli sometimes monoverticillate, usually branched and often consisting of the main axis and one branch (or metula) closely appressed, sometimes consisting of 3 or 4, more or less equal metulae, bearing clusters of sterigmata with conidia in loose tangled chains up to 150μ in length; branches (or metulae) 10 to 20μ by 2.2 to 3.0μ; sterigmata mostly in verticils of 3 to 7, closely

packed, 8 to 10μ by 2.2 to 2.8μ, without definite conidium-bearing tubes; conidia elliptical, mostly 3.0 to 3.5μ by 2.5 to 2.8μ but variable in the same mount and sometimes showing individual cells up to 7 or 8μ by 3.5 to 4.5μ, smooth-walled, often adherent in long chains in fluid mounts. Perithecia abundantly produced, appearing in central colony areas after 4 to 5 days and developing progressively with the enlargement of the colony, spherical to more or less oblong (fig. 71C) ranging from 100 to 200μ in diameter, composed of heavy-walled parenchyma-like cells, sclerotioid, ripening slowly from the center outward, developing limited asci and ascospores after four weeks or more, asci arising as branches from fertile hyphae often appearing in short chains, 10 to 12μ in diameter when mature, 8-spored; ascospores broadly elliptical, about 5.0 to 5.5μ by 4.0 to 4.5μ, occasionally up to 6.0 or 6.5μ in long axis, showing two prominent equatorial ridges, about 0.5 to 1.0μ in width, usually close together and sometimes appearing as a single ridge, as illustrated by van Beyma, convex spore surfaces definitely roughened (fig. 71D).

Colonies on steep agar essentially as on Czapek but growing more rapidly, developing abundant perithecia within 7 to 8 days, penicilli very few in number; ascosporic stage as on Czapek.

Colonies on malt agar attaining a diameter of 4.0 to 5.0 cm. in 12 to 14 days, plane, thin, consisting of a dense layer of perithecia (fig. 71B), completely covering the agar surface in the colony center but at times partially obscured by a limited development of aerial hyphae, colony surface appearing somewhat granular; penicilli more abundantly produced than on Czapek but similar in form and dimensions, conidiophores generally shorter; ascosporic stage as on Czapek but developing ripe asci and ascospores within 3 to 4 weeks.

Species description based upon van Beyma's type, received in December 1945, from the Centraalbureau and subsequently entered in our Collection as NRRL 2086. The type was isolated originally from soil collected at Baarn, Netherlands. The above species description agrees closely with van Beyma's original diagnosis except that he reported perithecia ranging from 200 to 300μ in diameter and described and illustrated ascospores as smooth-walled and showing a single prominent equatorial crest.

The perithecium of *Penicillium baarnense* van Beyma develops first as a sclerotioid mass of thick-walled, parenchyma-like cells. Subsequently there develops in the central area of this mass an extensive, closely interwoven mycelial network which frequently slips out as a unit when the outer crust of the perithecium, still somewhat sclerotioid, is broken up. The asci seem to develop at irregular intervals on this mycelium and to be clustered to a considerable degree. They appear to develop as lateral branches and when floating free are commonly seen in short chains

of rarely more than three asci. The manner of attachment to the mycelium has not been established nor is it clear whether, in time, asci develop more abundantly from hyphae at first showing scattered asci only. In his description of *P. javanicum*, van Beyma (1929) referred to the presence of a "skein" which we interpret to mean the network of hyphae upon which the abundant asci of that species are borne. The same hyphal network is seen in other species showing the initially firm or sclerotioid type of perithecium, but in no species is it more extensive than in *P. baarnense*. In *P. egyptiacum* van Beyma such a network is clearly evident, and in amount is somewhat intermediate between *P. javanicum* and *P. baarnense*.

True monoverticillate penicilli are sometimes produced in *Penicillium baarnense*, but these represent the exception rather than the general rule. The species is accordingly assigned with *P. egyptiacum* and *P. asperum* as a constituent member of the Carpenteles series.

Penicillium (*Carpenteles*) *euglaucum* van Beyma (Antonie van Leeuwenhoek **6:** 268–270, figs. 3–4. 1939/40), as represented by the type strain received in December 1945 from the Centraalbureau, duplicates the above in all essential characters. This species was based upon a culture isolated by Dr. Marie Ledeboer, Natal, South Africa, from the bark of an acacia tree. It was originally described by van Beyma as characterized by small, smooth, globose conidia 2.0 to 2.3 or even 2.7μ in diameter, (appearing rough with oil immersion), and ascospores 3.0 to 4.0μ by 3.0 to 3.3μ, slightly roughened, and showing a definite equatorial band. In our cultures both the conidia and the ascospores of the type, now maintained as NRRL 2087, duplicate those of *P. baarnense* as described above. Furthermore, the two types are strikingly similar in plate cultures upon many different substrata. It seems unlikely that the culture received as *P.* (*C.*) *euglaucum* is not the strain studied originally by van Beyma, since it agrees with his description in most particulars. We are led to believe that the species should be regarded as synonymous with *P. baarnense*, and that it differs from the latter only within the limits of normal strain variation.

Penicillium egyptiacum van Beyma, in Zentbl. f. Bakt. etc. (II) **88:** 137–138, figs. 6 and 7. 1933. See also Emmons, in Mycologia **27:** 143–144, figs. 6, 9, and 16. 1935; and Sabet, in Zentbl. f. Bakt. etc. (II) **94:** 97–102, figs. 1 and 6. 1936:

Colonies on Czapek's solution agar growing fairly rapidly, attaining a diameter of 4.0 to 4.5 cm. in 12 to 14 days at room temperature (fig. 72A), somewhat radially furrowed, comparatively deep, up to 1 mm. or more in central to subcentral areas, with surface loose-textured to floccose, predominantly white to cream colored, broadly zonate in some strains, azonate in others; conidial structures more or less concentrated in sub-marginal areas in some strains, light b'ue-green near gnaphalium green (Ridgway, Pl. XLVII), in other strains not produced in sufficient numbers to influence colony appearance; perithecia abundantly produced in some strains, not in others, when massed appearing granu'ar and tan to avellaneous in color;

FIG. 72. *Penicillium egyptiacum* v. Beyma. *A* and *B*, Two-week-old colonies of strain NRRL 1022 on Czapek and malt agars. *C*, Colony margin showing a characteristic penicillus and young perithecia, × 95. *D*, Detail of penicillus, × 1000. *E*, Perithecia as seen under low power, × 40. *F*, Ripe ascospores of strain NRRL 716, × 1500; note characteristic furrows in spores marked by arrows.

exudate lacking in most strains, abundant in others, clear to light straw colored; odor definite to pronounced, earthy; reverse at first uncolored, subsequently becoming dull orange-yellow near cinnamon to clay color (R., Pl. XXIX); penicilli variable in form, mostly biverticillate and asymmetric, arising mostly from the substratum or the basal felt, less commonly monoverticillate and borne on short branches from loose aerial hyphae (fig. 72C), biverticillate structures commonly consisting of a terminal group of metulae arranged in a true verticil, or arising at somewhat different levels, occasionally branched with each branch bearing metulae and sterigmata; conidiophores extremely variable in length, from 50 to 100μ when borne as branches from aerial hyphae up to 400 or 500μ when arising from the substratum by 2.5 to 3.0μ in diameter, smooth-walled; branches, when present, 10 to 15μ or more in length; metulae 2 to 5 in number usually 10 to 15μ by 2.2 to 2.8μ; sterigmata parallel, in compact clusters of 4 to 8, mostly 8 to 10μ by 1.8 to 2.2μ, with tips slightly narrowed (fig. 72D); conidia globose to subglobose, mostly 2.2 to 3.0μ, smooth-walled in loose tangled chains up to 100μ in length. Perithecia spherical to oblong (fig. 72E), from 100 to 225μ in diameter, maturing rather quickly, at first composed of heavy-walled parenchyma-like cells throughout, firm but not sclerotioid as in other members of the series, ripening from the center outward, developing a network of fertile hyphae bearing asci in definite chains, producing ripe asci and ascospores in two to three weeks and in 5 to 6 weeks completely filling the perithecium leaving only an outer wall 1 to 2 cells thick; asci oval to elongate, mostly 7.0 to 7.5μ in diameter, 8-spored; ascospores broadly lenticular, mostly 2.8 to 3.3μ by 2.2 to 2.8μ with equatorial areas flattened (fig. 72F) or showing two rather widely separated, low equatorial ridges, commonly lending to the spore a cask or barrel-like profile as noted by van Beyma.

Colonies on steep agar as on Czapek but growing somewhat more rapidly up to 5.5 to 6.0 cm. in 12 to 14 days at room temperature, in texture and pattern as above, conidial structures as described but generally more abundant; ascosporic stage essentially as described above.

Colonies on malt agar as on Czapek in rate of growth, not furrowed, usually heavier sporing, more commonly zonate, usually producing perithecia more abundantly (fig. 72B); details of conidial and ascosporic stages as described above.

Species description based upon van Beyma's type received in December 1945, from the Centraalbureau and subsequently incorporated in our Collection as NRRL 2090. Duplicated also by NRRL 1022 received in 1933 from Baarn and probably representing the same original strain; and NRRL 1023, received in 1934 from Dr. Rhoda H. Benham, Vanderbilt Clinic, New York City. NRRL 716, received in 1934 from Ross W.

Davidson, Division of Forest Pathology, U. S. Department of Agriculture, as an unidentified ascosporic *Penicillium*, differs from the above in producing colonies with fewer conidial structures, more abundant perithecia upon all media, and ascospores that appear less conspicuously ridged than those of the type strain. The culture, however, may be regarded as typical of the species.

Our observations are generally in close agreement with van Beyma's and the species diagnosis presented above differs little from the original description.

The type culture was isolated from soil in 1932 by Professor Y. S. Sabet at Cairo, Egypt, and was submitted to van Beyma who described the form as a new species, *Penicillium egyptiacum* (1933). Two additional isolations were made from Egyptian soil by Sabet (1935). The species has been isolated by other workers since that time and is believed to be cosmopolitan in distribution. When first isolated, the type produced perithecia very abundantly. Sabet (1936) reported a tendency toward the development of sectors marked by increased conidium and reduced perithecium formation and succeeded in separating out a sub-strain which was predominantly conidial and showed only a feeble capacity to form perithecia. During the period that the type has been maintained in artificial culture, both at Baarn and in our laboratory, it has become predominantly conidial but still retains the capacity to produce fertile perithecia. By selective recultivation in the present study we have succeeded in reisolating a predominantly perithecial strain which apparently closely approximates the type in its original form. NRRL 716, maintained in laboratory culture since 1934, has consistently produced abundant perithecia.

The perithecia of *Penicillium egyptiacum* strongly resemble those of the *P. javanicum* series in the Monoverticillata both in initial structure and in the manner in which they mature. The penicilli, however, are typically biverticillately asymmetric with monoverticillate penicilli present but obviously representing reduced structures. The perithecium ripens from the center outward by the development of a network of fertile hyphae which gradually replaces the parenchymatous to somewhat sclerotioid tissue. Asci are borne in chains, and develop more quickly and more abundantly than in either *P. baarnense* or *P. asperum*.

Occurrence and Significance

Members of the so-called *Carpenteles* series are known only as isolates from soil where they appear to be widely but not abundantly distributed. Their possible role in microbiological processes in nature is unknown. They are of interest primarily because of their ascosporic phase.

Sabet (1935) discussed the locales from which he isolated *Penicillium egyptiacum* and subsequently studied in some detail the cultural and morphological characteristics (1936) and the nutritional requirements of this fungus (1938). Cultures developed conidiophores in large numbers but produced few perithecia in media containing one per cent NH_4Cl as a source of nitrogen. Growth was arrested in media containing asparagine and few perithecia were produced. The mold showed no significant differences in growth within a pH range of 3.8 to 8.8 but perithecia developed later on the most alkaline media.

Penicillium raistrickii Series

Outstanding Characters

Sclerotia characteristically produced, ranging from very hard, well organized structures in some forms to irregular, comparatively soft masses of thick-walled pseudoparenchymatous cells in others.

Colonies growing rather rapidly upon most substrata, in some members developing abundant sclerotia which may markedly influence the colony appearance, in others producing sclerotia less abundantly and these commonly obscured by an overgrowth of conidial heads and vegetative mycelium.

Conidial structures usually abundant with conidiophores arising mostly from the substratum to produce a velvety effect in heavily sporing areas, commonly up to 250 to 400μ or more in length, with walls typically roughened, often conspicuously so.

Penicilli typically biverticillate and asymmetrical, commonly consisting of terminal verticils of 3 to 5 metulae, usually somewhat divergent hence suggesting clusters of separate monoverticillate penicilli under low magnification.

Conidia typically globose to subglobose, mostly 2.0 to 3.0μ in diameter, with walls generally smooth or nearly so.

Series Key

1. Conidial areas velvety or nearly so upon most substrata, conidiophores arising from the substratum or from aerial hyphae..... *P. raistrickii* series
   a. Conidiophore walls coarsely roughened, sclerotia well organized, firm or stony.
      1′. Sclerotia very hard, stony, white to light pink in color, vegetative mycelium white..... *P. raistrickii* Smith
      2′. Sclerotia fairly firm, not sclerotioid, yellow to light brown in color, vegetative mycelium often developing yellow shades from encrustment with yellow granules..... *P. pulvillorum* Turfitt
   b. Conidiophore walls finely roughened, true sclerotia lacking but small rounded masses of thick-walled cells evident upon all substrata and particularly upon malt agar..... *P. soppi* Zaleski

c. Conidiophore walls smooth or nearly so.
1′. White to pink sclerotia reported ..... *P. rolfsii* Thom
2′. Small masses of heavy-walled cells (as in *P. soppi*) produced in some strains. *P. miczynskii* Zaleski
(see *P. janthinellum* series)
2. Conidial areas commonly showing fasciculation, with conidiophores aggregated into more or less well defined bundles or tufts ..... *P. gladioli* Machacek
P. italicum Wehmer
(in the Fasciculata)

This series is characterized particularly by the formation of true sclerotia or sclerotia-like masses of thick-walled cells, the production of biverticillate and asymmetric penicilli, and a lack of any tendency toward fasciculation. Four species are included, namely: *Penicillium raistrickii* Smith, *P. pulvillorum* Turfitt, *P. soppi* Zaleski, and *P. rolfsii* Thom. Close genetic relationship between these forms is not assumed, and the four species are considered together principally as a matter of convenience. All produce penicilli that typically consist of terminal verticils of rather divergent metulae, hence are properly assignable to the Divaricata.

The sclerotia, or sclerotia-like cellular masses, differ substantially in the different species. In *Penicillium raistrickii* these are mostly rounded, very hard and gritty, naked or nearly so (fig. 73C), and withal bear a striking resemblance to the flesh to pink colored sclerotia produced by *P. thomii*, in the Monoverticillata (fig. 44D). In *P. pulvillorum* the cellular masses are less regular in outline, often larger, firm but not stone-like, and are commonly surrounded by a loose network of encrusted vegetative hyphae which lends a golden yellow to brownish coloration to the colonies on many substrata. The aggregates of heavy-walled sterile cells seen in *P. soppi* (fig. 75) are unusual among the Penicillia. These small masses suggest the beginnings of sclerotia, or possibly perithecia, but never develop into the large masses of cells that usually characterize these structures. They are regularly produced adjacent to the substratum and are generally obscured by an overgrowth of mycelium and abundant conidial structures, being apparent, as a rule, only along the interface of adjacent colonies. They seldom exceed 60 to 70μ in diameter and in the authors' experience seem to parallel the small aggregates of hülle cells produced in *Aspergillus granulosus* Raper and Thom (1944). Exact identity of the cellular elements in the two cases is not claimed, but the similarity in appearance is most striking. *Penicillium rolfsii* is included here primarily because Thom (1910), in his original diagnosis, reported the production of white to pink sclerotia ranging from elliptical to globose in form.

None of the members of the series appear to be abundant in nature.

Whereas the degree of relationship between the above forms and the members of the ascosporic Carpenteles series is somewhat uncertain, the

penicilli produced in the two series are sufficiently similar to warrant placing them in juxtaposition in a system of classification based primarily upon the pattern of conidial structures. Furthermore, the true sclerotia developed in *Penicillium raistrickii* of this series strikingly resemble the sclerotioid, late-ripening perithecia seen in *P. asperum* and *P. baarnense* in the Carpenteles series, and seem to differ from the latter principally in the fact that they consistently fail to develop an ascogenous stage.

Penicillium raistrickii Smith, in Trans. Brit. Myc. Soc. **18:** 90, Pl. IV, fig. 4, Pl. V, figs. 5 and 6. 1933.

Smith's diagnosis as follows:

"Colonies growing rapidly on most media at temperatures up to 30°C., rate of growth much less above 30°C. and nil at 37°C.; bluish green, then greyish green, and finally somewhat brown, velvety; reverse persistently uncoloured, showing masses of sclerotia; conidiophores arising from the substratum, up to 250μ long, 3.5 to 4.0μ in diameter, rough; penicilli typically divaricate, comprising 3 to 5 monoverticillate heads united into a fairly compact whole; metulae clavate, sometimes very slightly roughened, 10 to 13μ by 4.0 to 4.8μ; sterigmata closely packed on each individual metula, 7.5 to 9.0μ by 2.6 to 3.0μ; conidia globose or nearly so, smooth, 2.2 to 2.7μ in diameter, conidial chains packed into diverging solid columns; sclerotia produced abundantly, hard, feeling like grit under a cover-glass, consisting of masses of irregular-shaped thick-walled cells, white to dirty white, globose or ovoid, up to 180μ in long axis.

"This species is noteworthy chiefly on account of its very free production of sclerotia."

Our notes follow:

Colonies on Czapek's solution agar about 3.0 cm. in 12 to 14 days at room temperature, velvety, usually producing abundant conidial structures arising primarily from the substratum, in blue-green shades near dark glaucous gray (Ridgway, Pl. XLVII), azonate or slightly zonate, lightly furrowed in a predominantly radial pattern (fig. 73A), showing some tendency toward sector variation, developing limited areas almost floccose and bearing conidial structures from aerial hyphae; limited clear exudate produced; odor lacking; reverse uncolored to vinaceous drab shades; details of the penicillus as described by Smith except conidia commonly appear elliptical and range up to 3.0 to 3.3μ in diameter; developing abundant sclerotia (fig. 73C) throughout the entire colony (see above) and often characterizing its appearance.

Colonies on steep agar growing more rapidly, 4.0 to 4.5 cm. in 12 to 14 days, in color and texture as on Czapek but with reverse in orange-brown shades and surrounding agar uncolored.

Colonies on malt agar spreading, about 4.5 cm. in two weeks (fig. 73B), plane, often showing a marked tendency to sector, with some areas heavy-

sporing in blue-green shades as on Czapek, adjacent sectors predominantly sclerotial and appearing light buff from the production of sclerotia and increased sterile hyphae; reverse in golden to dull brown shades.

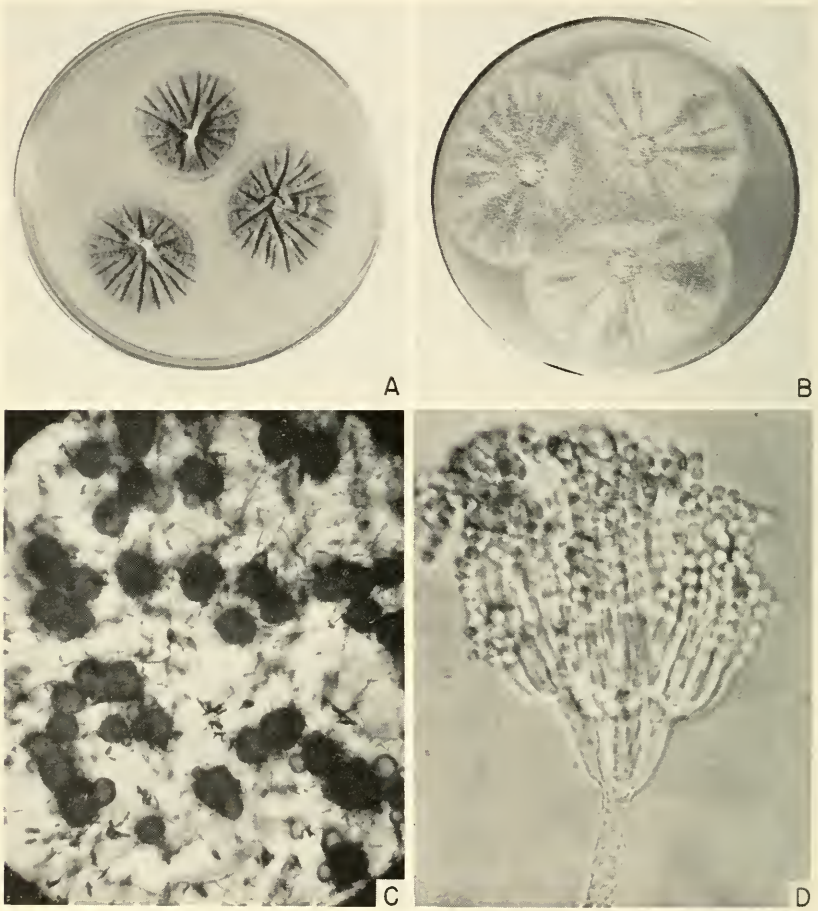


FIG. 73. *Penicillium raistrickii* Smith, NRRL 2039. *A* and *B*, Ten-day-old colonies on Czapek and malt agars. *C*, Marginal area showing sclerotia and penicilli intermixed, × 40. *D*, Detail of a single and unusually compact penicillus, × 1000.

Cultural notes taken from the type strain isolated by George Smith (catalogue No. 100) from moldy cotton yarn in the period between 1927 and 1929. The species is noteworthy for its free production of sclerotia as pointed out by the describer, and also for its unusually rough-walled conidiophores. The type culture is maintained in our collection as NRRL 1044, received from Smith in 1933, and as NRRL 2039, received more

PLATE V

TOP: Penicillium asperum (Shear) n. comb, NRRL 2088, on steep agar, 10 days. *CENTER: Penicillium janthinellum* Biourge, NRRL 2016, on Czapek's solution agar, 10 days. *BOTTOM: Penicillium nigricans* (Bainier) Thom, NRRL 915, on Czapek's solution agar, 12 days. (Color photographs by Haines, Northern Regional Research Laboratory. Reproduced through co-operation of Chas. Pfizer & Co., Inc.)

recently from the National Collection of Type Cultures in London. The sub-strains remain identical.

In the compact nature of its penicillus (fig. 73D) and in the well-developed columns of conidia arising from the metulae which comprise it, *Penicillium raistrickii* is somewhat suggestive of *P. citrinum* Thom. It differs from the latter form, however, by its production of sclerotia, which have not been reported for the *P. citrinum* series, and in its very rough-walled conidiophores, which are in striking contrast to the smooth-walled structures in *P. citrinum*. The sclerotia produced are strongly suggestive of those seen in *P. thomii* Maire both in form and texture. Close relationship of the two species is not presumed, however, because of the marked differences in their penicilli.

Penicillium howardii Thom (The Penicillia, p. 368. 1930) was described very briefly and sufficient information was not given to adequately characterize the colonies produced. While one cannot, with certainty, regard this species as synonymous with *P. raistrickii*, it is believed to have approximated it, even though sclerotia were not reported, since conidiophores of *P. howardii* were described as rough, bearing penicilli which consisted of 3 to 4 metulae, 10 to 13μ long, with long, dense, divergent columns of conidia. The species has not been subsequently reported and probably should be dropped.

Penicillium pulvillorum Turfitt, in Brit. Myc. Soc. Trans. **23:** 186–187, Pl. IV, figs. 1 and 2. 1939.

Turfitt's diagnosis follows:

"Colonies on Czapek agar at 24°, matted floccose, often radiately wrinkled, spreading, becoming 35–40 mm. in diameter, 0.5–1 mm. deep in 8 days; marginal zone raised, white, passing later to brownish shades, 3–5 mm. wide; conidial areas at first pale green, becoming deeper green, clearly zonate towards the growing edge with zones about 2 mm. apart, gradually turning brownish from centre outwards with development of sclerotia; reverse colourless at first, then somewhat zonate in pale yellow shades, becoming deeper yellow and brownish in age; odour none; conidiophores commonly arising as short branches from trailing hyphae, 1.5–3μ in diameter, with walls markedly roughened; penicilli occasionally as single verticils of sterigmata, usually divaricate with terminal groups of 2–3 metulae, and with secondary penicilli, mostly monoverticillate, arising from lower nodes of main axis; metulae mostly 3–3.5μ in diameter, varying greatly in length, 12–25μ; sterigmata 8–10 x 2.5–3μ, sharp-pointed, with conidial chains roughly parallel or more or less divergent, becoming tangled in age; conidia 2.5–3μ in diameter, smooth, globose; sclerotia very abundant, forming early amongst superficial growth of trailing and anastomosing hyphae, yellow-brown, irregular in shape, very variable in size, averaging 700μ in diameter, consisting of compact hyphal masses, remaining soft; development of asci not observed."

In his original paper, Turfitt noted that "the fungus grows almost equally well on wort and Czapek agar, and the appearance of the colonies on both media is closely similar." In our cultures of Turfitt's type strain

(now maintained as NRRL 2026), received from the Centraalbureau in May 1946, colonies on Czapek's solution and malt extract agar (approximates wort) differ substantially.

On Czapek the colonies are somewhat radially furrowed, close-textured (fig. 74A) and consist of a tough basal felt in which are embedded abundant small irregular, yellow to light brown sclerotia mostly 100μ or less (fig.

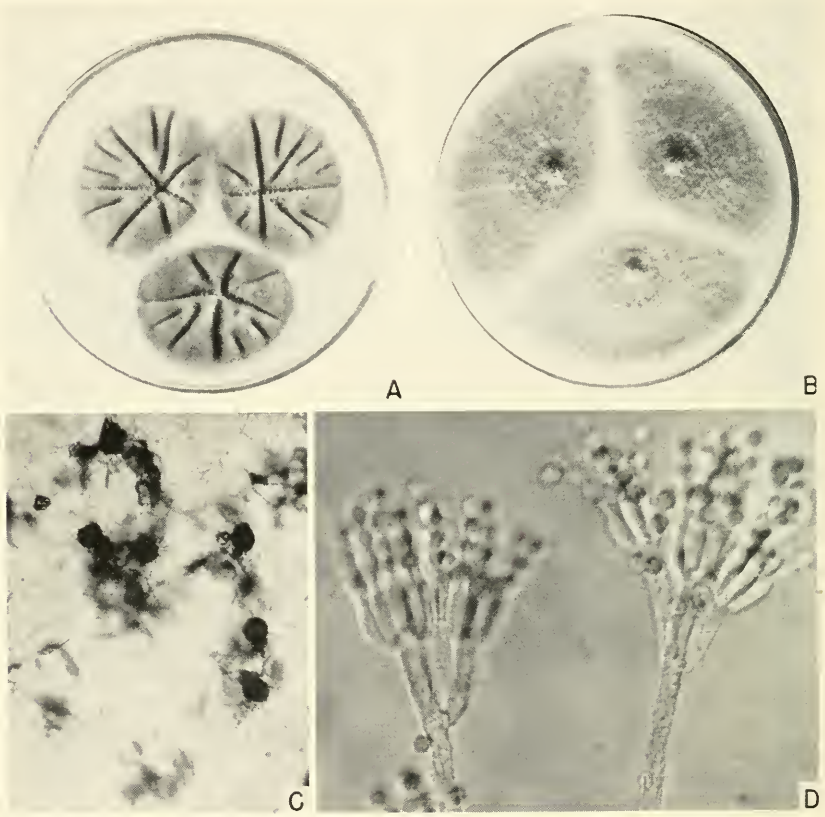


FIG. 74. *Penicillium pulvillorum* Turfitt. *A* and *B*, Two-week-old colonies of NRRL 2081 on Czapek and malt agars. *C*, Scattered sclerotia of NRRL 2082, × 40. *D*, Detail of penicilli in same strain, × 1000.

74C), and with colony surface characterized by a thin, more or less floccose overgrowth from which scattered to fairly abundant divaricate conidial structures develop, with large structures arising from the substratum directly; conidiophores conspicuously rough, up to 400 to 500μ in length by 3.0 to 3.5μ in diameter; penicilli as described by Turfitt (fig. 74D).

Colonies on steep agar essentially as on Czapek but growing more

rapidly, more conspicuously furrowed, and bearing more abundant sclerotia, occasionally up to 200μ in diameter. Heavier sporing than above but with structural details essentially the same.

Colonies on malt agar growing more restrictedly, in some strains, spreading broadly in others (fig. 74B), plane, consisting of a dense layer of larger, yellow to very light brown sclerotia overgrown by a loose network of interlacing hyphae; conidiophores arising mostly from the substratum, commonly 500μ or more in length by 3.0 to 3.5μ, bearing large asymmetric, usually divaricate, penicilli; conidia delicately roughened but in size and form as described by Turfitt; sclerotia rarely exceeding 250μ in diameter, more commonly about 150μ. Colonies in reverse in reddish shades approximating coral-red (Ridgway, Pl. XIII).

The type strain was isolated by Turfitt from acid soil collected in London.

Two additional strains duplicating the type have been examined. The first of these, NRRL 2082, was received in February 1944, from Dr. Jackson W. Foster, Merck and Company, as an unidentified *Penicillium;* the second, NRRL 2081, was isolated from a sample of soil sent by Dr. A. G. Kevorkian from Nicaragua, and differs from the above only in producing more abundant yellow-encrusted sterile hyphae surrounding the sclerotia.

In describing *Penicillium pulvillorum*, Turfitt (1939) called attention to the soft character of the sclerotia in his species and contrasted these with the hard structures typical of *P. raistrickii* Smith and *P. thomii* Maire. While there is a marked difference between the sclerotia of these species, it is not as pronounced as Turfitt's description would seem to indicate. In our experience, the sclerotia of *P. pulvillorum*, while not hard and gritty, are, nevertheless, quite firm and withstand considerable pressure without collapsing. They are quite variable in form and dimensions, and appear somewhat intermediate between the rounded, very hard sclerotia of *P. raistrickii* and the small, less definitely organized cellular masses seen in *P. soppi.* In form and texture, the sclerotia of *P. pulvillorum* are suggestive of the perithecia of certain species such as *P. brefeldianum* or *P. javanicum;* but confirming Turfitt's observations, no evidence of ascospore formation has been seen.

Penicillium soppi Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B., pp. 476–477, Taf. 51. 1927; see also Thom, The Penicillia, pp. 344–345. 1930.

Colonies on Czapek's solution agar somewhat restricted, attaining a diameter of 3.0 to 3.5 cm. in 10 to 12 days at 24°C., consisting of a close-textured basal felt with loose surface overgrowth up to 500μ or more deep,

almost lanose, radiately wrinkled (fig. 75A), at first white, gradually developing conidial structures after one week, thinly scattered throughout but produced more abundantly near the colony margin and particularly adjacent to the intercolony area, in pale gray-green shades near gnaphalium green (Ridgway, Pl. XLVII); odor lacking or indefinite; exudate limited to abundant, clear; reverse uncolored to pale peach; with thick-walled, sterile cells in small masses up to 50 to 60μ in diameter, suggesting small sclerotia (fig. 75D), occurring adjacent to the substratum throughout the colonies but most abundantly along the intercolony margins, resembling fine white sand in appearance (fig. 75C) but not firm or gritty; penicilli borne upon long conidiophores with walls finely roughened, up to 1 mm. by about 2.5 to 3.0μ, arising from the substratum along intercolony margins and upon branches of variable length arising from aerial hyphae in central colony areas; penicilli variable, in large structures usually consisting of a terminal verticil of 3 to 5 metulae (fig. 75F), 8 to 12μ by 2.5 to 3.0μ, enlarging upward, each bearing clusters of 5 to 8 closely crowded sterigmata, not strongly divaricate but with individual metulae having the appearance of monoverticillate penicilli, in smaller structures usually consisting of 2 or 3 metulae which may or may not be borne at the same level; sterigmata mostly 6 to 8μ by 2.0μ with conidium-bearing tips short, not pronounced; conidia at first elliptical, becoming globose to subglobose at maturity, mostly 2.5 to 3.0μ in diameter, with surface smooth or very delicately roughened.

Colonies on steep agar 5.0 to 5.5 cm. in 10 to 12 days, approximately 1 mm. deep, loose-textured with surface appearing lanose, heavily sporulating throughout, gnaphalium green in mature conidial areas (R., Pl. XLVII); exudate limited; numerous sclerotia-like masses produced; penicilli mostly borne upon long, erect conidiophores and generally larger than on Czapek but of the same basic pattern.

Colonies on malt extract agar spreading, 6 to 8 cm. in 12 days at 24° C., thin, very loose, floccose, medium sporulating throughout; with small masses of sterile cells abundantly produced adjacent to the substratum (fig. 75B); penicilli as described above; no exudate; reverse in dull brown shades, usually producing a zone of more intense color at the colony margin in age.

Species description based primarily on NRRL 2023, received in May 1946, from the Centraalbureau as Zaleski's type strain. Also representative of the species is a culture received from Baarn as Zaleski's strain, presumably type, of *Penicillium matris-mcae*. In the latter culture, masses of thick-walled cells were scattered but present; and in cultural aspect it duplicated the preceding, even to the point of producing a marginal brown zone in malt agar plates. This same culture, NRRL 912, as maintained in

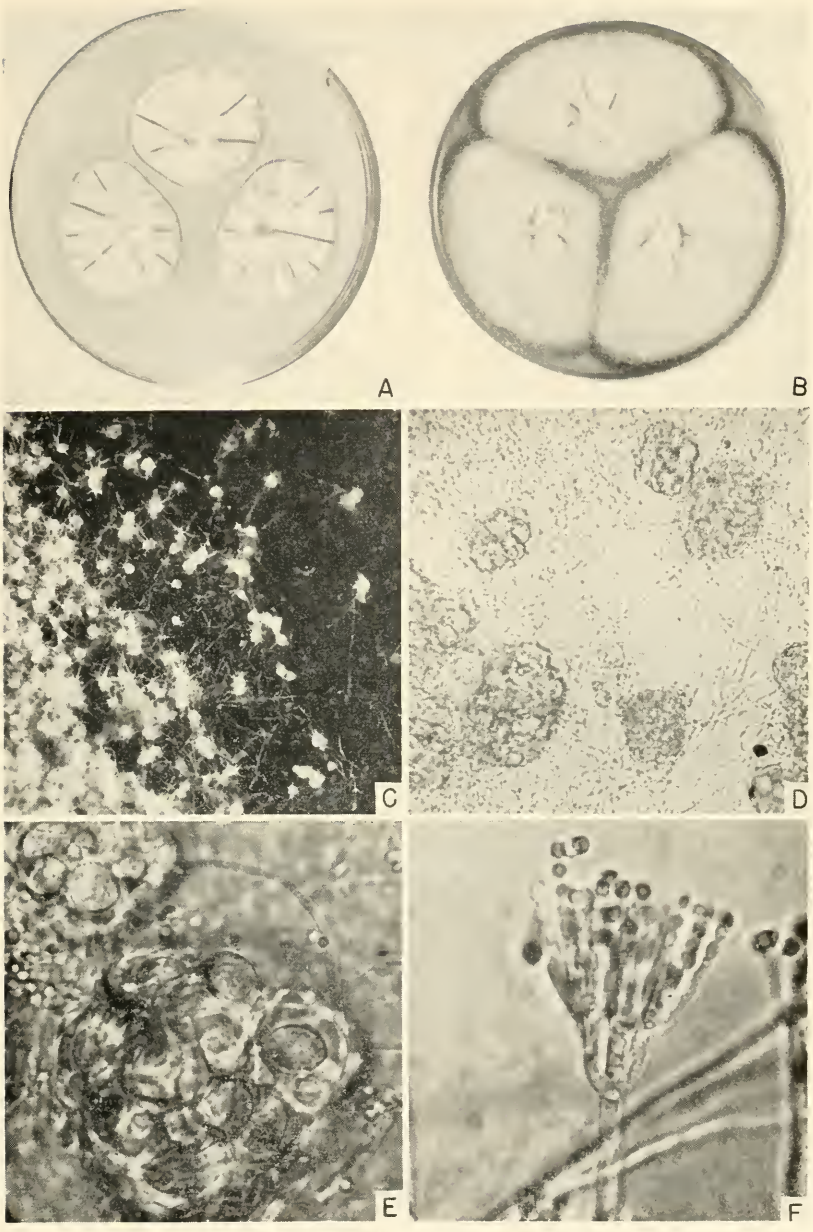


FIG. 75. *Penicillium soppi* Zaleski, NRRL 2023. *A* and *B*, Two-week-old colonies on Czapek and malt agars; note the characteristic dark marginal bands in the latter substrate. *C*, Colony margin on malt agar showing abundant clusters of thick-walled cells, × 30. *D*, The same somewhat enlarged, × 225. *E*, The same still further enlarged, × 700. *F*, Detail of penicillus, × 1300.

our laboratory since 1928, presented the same cultural picture as the two preceding cultures, but thus far, has failed to produce the characteristic masses of thick-walled cells although it too produces a marginal brown zone in malt agar.

In the type strain of *Penicillium soppi*, sclerotia-like structures are limited to small irregular masses of thick-walled parenchyma-like cells strongly suggestive of the hülle cells of some *Aspergilli* (fig. 75E), particularly *Aspergillus granulosus* Raper and Thom (1944). One culture, NRRL 701, has been examined which produces colonies and develops conidial structures essentially like NRRL 2023, but consistently produces abundant hard sclerotia upon all media employed. A decision as to whether this should be regarded as a new species, or the description of *P. soppi* broadened to include it, must await the examination of additional strains approximating the cultures in question. Also to be considered is the possibility that NRRL 701 represents in effect a variant of *P. raistrickii* Smith which fails to develop the typical rugose character of its conidiophores.

Thom (1930) placed *Penicillium soppi* Zaleski in his section Lanata-Divaricata upon the character of its penicilli which he noted as consisting of variously branching, divergent groups of 2 to several monoverticillate branches. This placement appears to be satisfactory, and the production of sclerotia-like masses of thick-walled cells seems to relate it particularly to the series embracing *P. pulvillorum* and *P. raistrickii*.

Penicillium matris-meae Zaleski (in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 477–479, Taf. 45 and 52. 1927) must be regarded as a synonym of his *P. soppi*. Careful examination of the descriptions of the two species reveals that they were described in almost identical terms, and no significant difference can be observed from his figures. The fact that two cultures, presumably Zaleski's type strains of *P. soppi* and *P. matris-meae*, proved to be exact duplicates further confirms the identity of the two species.

Penicillium rolfsii Thom, in U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118; pp. 80–81, fig. 36, 1910, as *Penicillium* No. 32. Described by Thom in The Penicillia, pp. 489–490, fig. 86. 1930.

Author's description (abstracted):

Colonies upon milk-sugar-gelatin and potato or bean agar gray-green; floccose, but with aerial part consisting mostly of long conidiophores and few vegetative hyphae, slightly yellowish to pronounced salmon color below; broadly spreading; developing white to pink elliptical to globose sclerotia 150 to 200μ in diameter at the surface of the substratum in 2 to 3 weeks; odor none; conidiophores 200 to 500μ by 3.0 to 4.0μ; penicilli consisting of verticils of 3 to 5 branches (metulae) 10 to 17μ by 2.0 to 3.0μ, rarely showing secondary verticils, each bearing a dense verticil of sterigmata,

8 to 10μ by 2.0μ, producing long, parallel, or slightly divergent chains of conidia; conidia elliptical or fusiform, 3.5 to 4.0μ by 2.0 to 3.0μ, green, granular within, smooth, swelling in germination to 6.0μ and producing from one to several germ tubes.

Sent by Prof. P. H. Rolfs from Miami, Florida, upon a portion of pineapple, March 1905.

Our notes follow:

Colonies on Czapek's solution agar in the current study differ from the above in producing comparatively few conidial structures upon a loose flocculent mycelial felt, in producing cream to light drab color in reverse, and in its failure to produce sclerotia. Penicilli are irregular in pattern and conform fairly closely with the original description; conidia are strongly elliptical and smooth-walled as described.

Colonies on steep agar are similar to the above but are heavier sporing and likewise fail to develop sclerotia.

Colonies on malt agar differ from the above in producing fairly abundant conidial structures in a layer near the substratum which becomes overgrown and largely obscured by a white flocculent overgrowth.

The above notes refer to the type strain, Thom's No. 32, received originally from Prof. Rolfs. It is now maintained in our Collection as NRRL 1078.

Some question exists as to the correct placement of this species. In his Monograph, Thom (1930) assigned this species to a miscellaneous series at the end of the Biverticillata-Symmetrica. This placement was based upon the irregularity of its conidial structures, plus a general lack of diagnostic features to place it in any well-recognized section of the genus.

Upon the basis of cultural characteristics, and the pattern structure of its penicilli and sterigmatic cells, the species is believed to be more properly assignable to the Divaricata than to any other section. The reported presence of white to pink sclerotia 150 to 200μ in diameter in the type, as originally described, further indicates relationship to the *Penicillium raistrickii* series as it is understood by us—hence, the present assignment.

No additional strains clearly representing this species have been encountered by us.

Occurrence and Significance

Penicillium raistrickii and allied species are encountered occasionally as isolates from soil or from soil contaminated materials, but nowhere seem to be abundant. Smith (1933) isolated *P. raistrickii* from moldy cotton yarn and attributed some damage as probably due to its presence. No biochemical or physiological studies are known to have been reported for members of the series.

Penicillium lilacinum Series

Outstanding Characters

Colonies typically loose-textured to floccose, growing rapidly, light to heavy sporing, in lilac to light vinaceous or avellaneous—never in green —shades.

Conidiophores varying greatly in length, arising from the substratum or as branches from ascending hyphae, with walls smooth or finely roughened.

Penicilli conspicuously divaricate, of variable dimensions, commonly consisting of terminal clusters of divergent metulae, or appearing as monoverticillate structures when borne on short branches from ascending conidiophores.

Sterigmata acuminate with spore-bearing tubes, typically long, thin, and pointed.

Conidia usually elliptical to lemon-shaped, commonly appearing apiculate, smooth-walled.

Series Key

A. Colonies not showing green, gray-green or blue-green with the ripening of conidia.
  1. Colonies deeply floccose, becoming lilac, vinaceous or violaceous with the development of conidia ..... *P. lilacinum* series
    a. Colonies developing lilacinus (Saccardo) or vinaceous (Ridgway) shades, with reverse similarly colored, or in some strains becoming purple-red. *P. lilacinum* Thom
    b. Colonies developing violet shades near "light lobelia violet" (Ridgway) with ripening of conidia and with reverse in bright yellow shades. *Spicaria violacea* Abbott
  2. Colonies not deeply floccose, comparatively thin, often strongly wrinkled, becoming pinkish-buff to avellaneous with ripening of conidia. *P. humuli* van Beyma
  3. Colonies velvety or nearly so, with conidial areas in tan, cream, or near-white shades, never showing green ..... Natural mutants of many species.

Strictly speaking, this series includes the single and rather easily recognizable species, *Penicillium lilacinum* Thom. Two additional species are considered with it as a matter of convenience. In these a degree of true relationship is suggested, but this remains to be established. The first of these, *P. humuli* v. Beyma, produces conidia in pale pinkish buff shades and normally shows penicilli that are strongly divaricate, usually consisting of a single verticil of 2 or 3 terminal metulae. Sterigmata are not as a rule conspicuously tapered or pointed, and mature conidia are normally subglobose to globose rather than elliptical.

The second species, *Spicaria violacea* Abbott, in its typical form, is clearly separable from *Penicillium lilacinum*. However, strains appar-

ently intermediate between these two species are so commonly encountered that *S. violacea* is included here, although described in another genus. Transfer of Abbott's species to the genus *Penicillium* has been considered but rejected since the conidial structures are so very variable in form, are in fact as often *Verticillium*-like as penicillate, and usually show very long, tapered sterigmata that are often extremely divaricate. If the genus *Spicaria* is valid, then it would seem that this species should remain assigned to it. There is the further possibility that *P. lilacinum* Thom properly belongs in *Spicaria*, although we feel its Penicillium-like characteristics justify its inclusion in any treatment of the genus *Penicillium*.

Penicillium lilacinum Thom, in U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, 73–75, fig. 30. 1910. See also, Thom, The Penicillia, pp. 331–334, figs. 49 and 50. 1930.

Colonies on Czapek's solution agar attaining a diameter of 3.0 cm. in 10 days at room temperature, floccose, loose-textured, commonly 1 to 2 mm. deep (fig. 77A), with central colony areas raised in some strains, not in others, irregularly showing few, shallow, radial furrows, azonate, at first white, gradually developing lilac to vinaceous shades near grayish vinaceous to purplish vinaceous (Ridgway, Pl. XXXIX) with the production and ripening of conidia, sporulation varying in different strains and often diminishing with continued laboratory cultivation, generally abundant; limited exudate produced, uncolored to vinaceous; odor slight or lacking; reverse at first uncolored, later usually showing vinaceous shades, and in some strains becoming strongly colored near daphne red to vernonia purple (R., Pl. XXXVIII); conidiophores varying greatly in dimensions (fig. 76), arising from the substratum at the colony margin (fig. 76B_1) and from aerial hyphae in central colony areas, the former ranging up to 500 or 600μ or more in length by 3.0 to 4.0μ wide, the latter ranging from very short, where the penicillus appears to arise almost directly from the supporting aerial hyphae (fig. 76B_2), up to 100 to 200μ by about 3.0μ, with walls smooth or appearing finely roughened (fig. 76B_3), colorless or in larger structures slightly yellowed; penicilli varying in size and complexity (fig. 76A), bearing tangled chains of conidia up to 50 to 75μ in length, not branched in the usual manner for the genus, in larger structures typically consisting of complete or partial whorls of metulae (or in largest structures of branches bearing metulae) arising at two or more levels (nodes) below the terminal clusters (fig. 76), up to 50μ or more in length, in smaller structures commonly consisting of a single verticil of metulae; metulae short, usually 5.0 or 6.0μ, occasionally 8.0μ in length by 2.5 to 3.0μ; sterigmata mostly 5.0 to 6.0μ in length abruptly tapering to a comparatively long, thin spore-bearing tube approximately 1.0μ in diam-

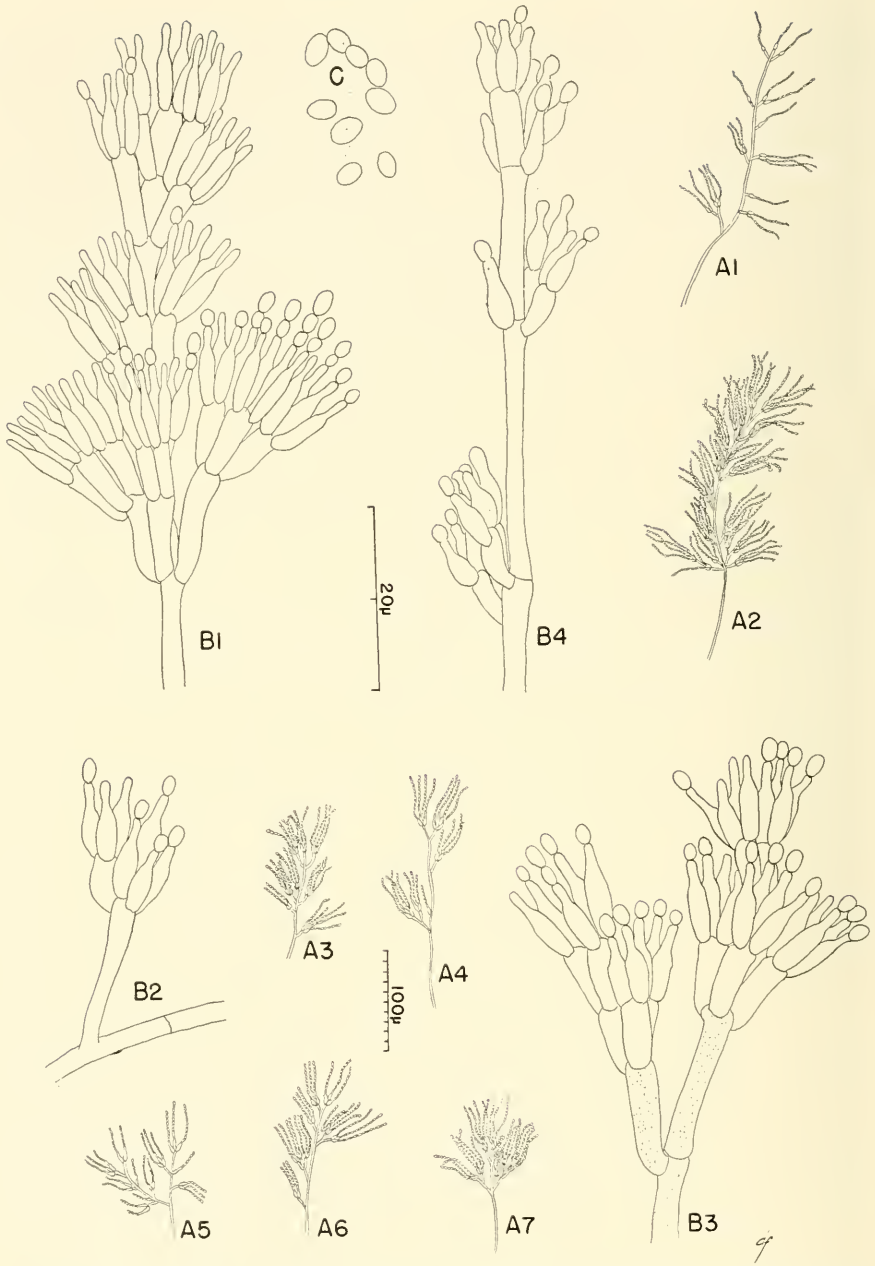


FIG. 76. *Penicillium lilacinum* Thom. A_1–A_7, Habit sketches of representative penicilli illustrating the range of patterns encountered. B_1–B_4, Penicilli as seen under oil immersion showing range of pattern and complexity, and illustrating details of cellular structure—note the slightly roughened conidiophores in B_3. *C*, Mature conidia.

eter and 2.0μ or more in length (fig. 76B_3); conidia elliptical, 2.5 to 3.0μ by 2.0μ, smooth-walled (fig. 76C), light vinaceous in mass.

Colonies on steep agar growing more rapidly, attaining a diameter of 4.0 to 4.5 cm. in 10 days at room temperature with texture and general colony appearance as on Czapek, generally heavier sporing, hence in darker shades; penicilli essentially duplicating those on Czapek's agar.

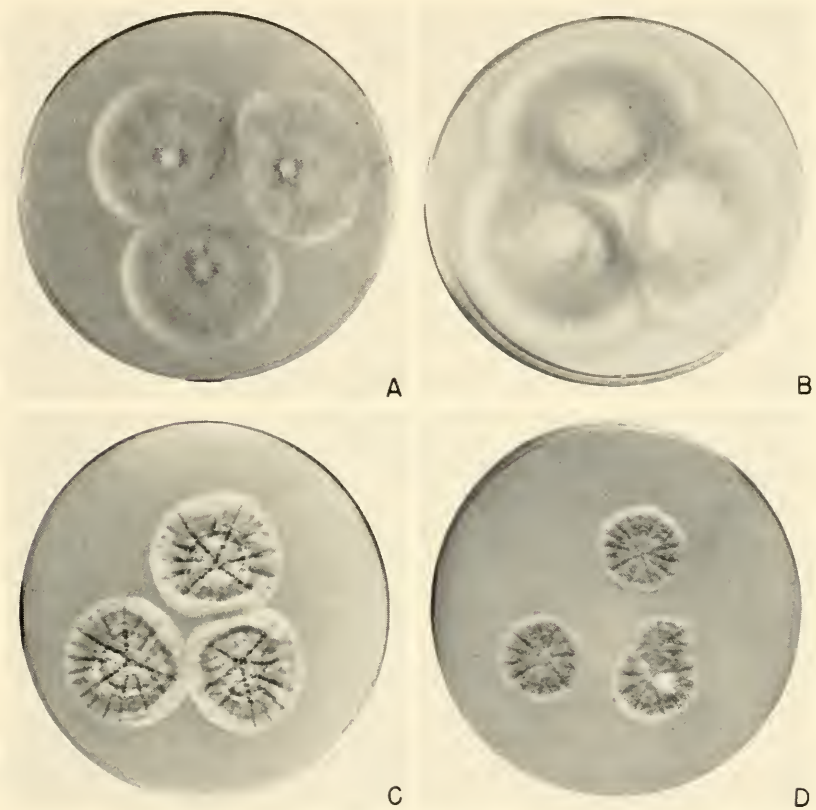


FIG. 77. *A* and *B*, *Penicillium lilacinum* Thom, NRRL 895, on Czapek and malt agars at ten days. *C* and *D*, *Spicaria violacea* Gilman and Abbott, NRRL 2015, on the same substrata, same age.

Colonies on malt agar as on Czapek's but generally more floccose, up to 5 or 6 mm. deep (fig. 77B), and with reverse commonly showing dark to almost black shades in central colony areas, penicilli as above.

Species description based upon NRRL 895 (Thom's No. 8), the type strain, and many additional cultures isolated by us from soil and other natural sources, as well as numerous accessions contributed by many

collaborators from all over the world. Among these NRRL 2014, isolated from Nicaragua soil in October 1945, may be regarded as representative.

Members of this series are among the most abundant of all the soil Penicillia. Individual strains differ from one another in rate of growth, colony appearance, amount of sporulation, and, to a lesser degree, in the character of their spore-bearing structures. These, however, are believed to represent only variant strains in a single cosmopolitan and unusually abundant species of saprophytic molds.

Under continued laboratory cultivation, strains commonly tend to become increasingly floccose and to lose their capacity to sporulate freely.

Penicillium amethystinum Wehmer (nomen nudum) was cited by Biourge (Monograph, La Cellule **33**: fasc. 1, pp. 221–222; Col. Pl. VI, Pl. X, fig. 56. 1923) as a synonym of *P.* (*Scopulariopsis*) *rubellum* Bainier. Two cultures apparently representing Biourge's concept of this species were received from him, labeled *P. amethystinum* Wehmer and *P. rubellum* Bainier. Both proved to be *P. lilacinum* Thom. Whereas the binomial *P. amethystinum* would be beautifully descriptive of certain members of the *P. lilacinum* series that produce exudate and colony reverse in bright reddish purple ("amethyst") shades, no description has been found to cover the use of this name by Wehmer, and recognition as a species separate from *P. lilacinum* is not warranted.

Spicaria violacea Abbott, in Iowa State College Jour. Sci. **1**: 26, fig. 3. 1926. See also Gilman and Abbott, Iowa State College Jour. Sci. **1**: 301. 1926; and Thom, The Penicillia, p. 335. 1930.

Colonies on Czapek's solution agar attaining a diameter of 3.0 to 3.5 cm. in 10 days at room temperature, floccose, loose-textured, 1 to 2 mm. or more deep (fig. 77C), with central colony areas commonly raised, radially furrowed in some strains, not in others, at first white but developing lavender or pale blue-violet shades (Ridgway, Pl. XXXVI) with the production of mature conidial structures, uniformly colored throughout or with marginal areas in deeper shades; odor indefinite or lacking; exudate lacking or limited, yellow to amber when present; reverse at first colorless but quickly assuming bright yellow shades with the surrounding agar usually colored in like manner. Conidial structures usually abundant, very irregular in size and pattern, verticillate or penicillate, with verticils of metulae and sterigmata present in large structures, or sterigmata only in smaller fruits, with elements strongly divergent (fig. 78) and with long conidial chains characteristically tangled in age. Conidial structures borne upon branches arising from aerial hyphae, often at successive levels, usually less than 100μ in length, or upon longer conidiophores up to 500μ by 2.5 to 3.0μ that arise directly from the substratum. Irrespective of its origin or complexity, the conidial apparatus is typically characterized by its strongly divergent aspect (fig. 78A) and its conspicuously tapered sterig-

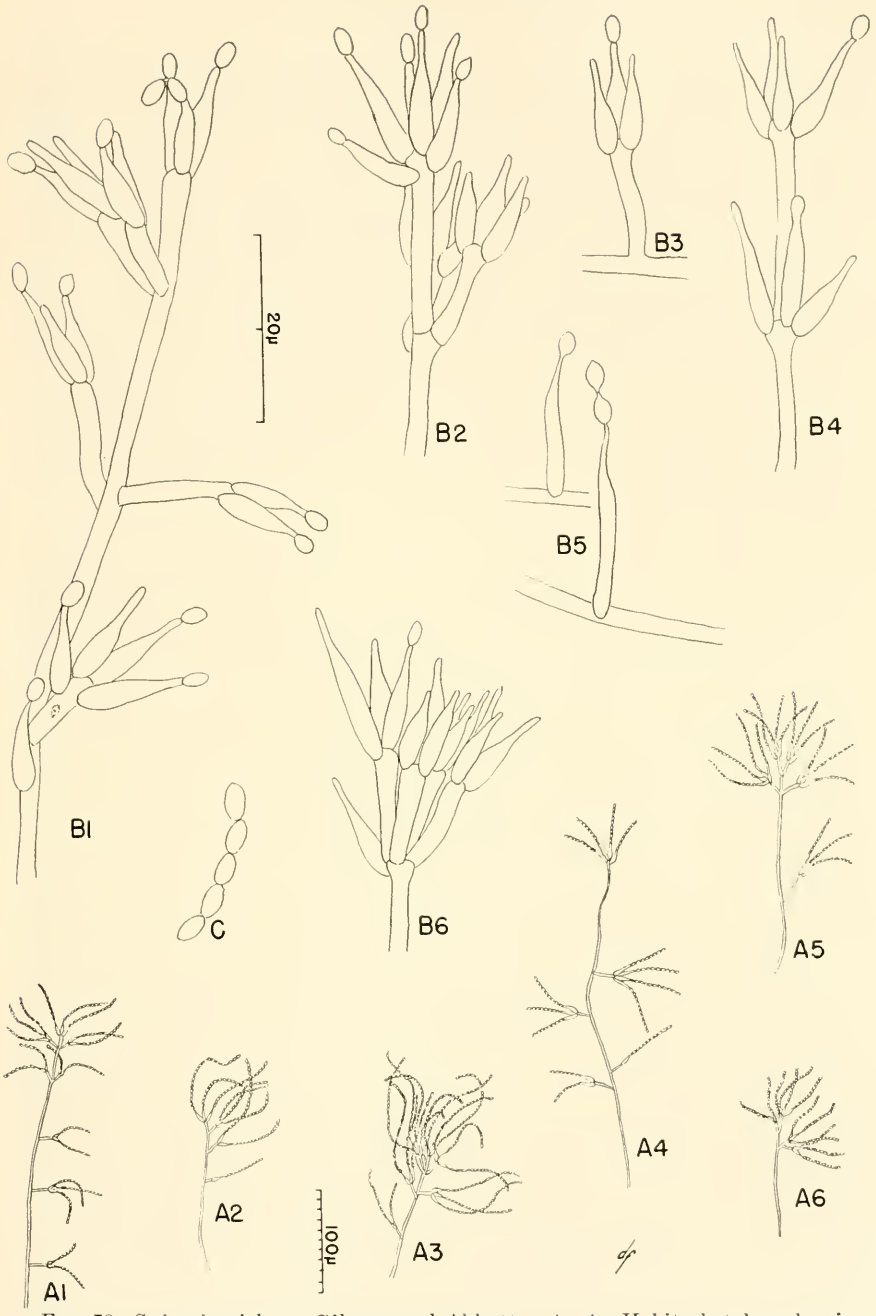


FIG. 78. *Spicaria violacea* Gilman and Abbott. A_1–A_6, Habit sketches showing variations in pattern and complexity of conidial structures. B_1–B_6, Enlarged views of similar structures. *C*, Mature conidia.

mata (fig. 78B). Dimensions of parts vary greatly in different fruits and sharp separation into metulae and sterigmata at specific levels is often lacking, but metulae usually occur in groups of 3 to 5 in larger structures and measure about 7 to 10μ by 2.0 to 2.5μ, and sterigmata in verticils of 3 to 7 and measure 8 to 10μ by about 2.0μ in width in the basal portion with the apical half tapering to a thin point-like tube, not exceeding 0.5μ in diameter, upon which the conidia are borne. Conidia strongly elliptical, with ends usually pointed, mostly 3.0 to 3.5μ by 2.0 to 2.5μ (fig. 78C), with walls smooth or finely roughened, pale vinaceous in mass.

Colonies on steep agar growing somewhat more rapidly, looser in texture, heavier sporing, at 10 days ranging in color from lavender to verbena violet (R., Pl. XXXVI), generally becoming more highly colored in age; exudate lacking or limited in amount; odor indefinite; reverse of colonies intense yellow with surrounding agar colored in the same shades; fruiting structures as described above.

Colonies on malt agar commonly smaller than the above (fig. 77D), loose-textured, conspicuously floccose in some strains, definitely thinner in others, medium to heavy sporing with conidial areas colored as on steep agar, reverse in bright yellow to golden yellow shades; fruiting structures as above but with conidial chains commonly longer.

Species description based upon the type strain NRRL 901 (Thom's No. 4894.4) isolated from soil and received from Gilman and Abbott in 1927. Represented also by numerous isolations and accessions subsequently studied, including NRRL 1770, a soil isolate from C. W. Hesseltine, University of Wisconsin; and NRRL 2015 isolated by us from soil from Mexico.

Spicaria violacea in its typical form is clearly distinct from *Penicillium lilacinum*. Conidial areas are in blue-violet rather than reddish violet (vinaceous) shades, colonies in reverse show bright yellow rather than vinaceous shades, and fruiting structures are typically more divergent and show sterigmata tapering more gradually to thinner conidium-bearing tips.

Many isolates, however, appear intermediate between strains that are typical of *Spicaria violacea* and others that are typical of *Penicillium lilacinum*. The relationship of the two forms is not entirely clear and there is some question whether the whole *P. lilacinum* series, exclusive of *P. humuli* v. Beyma, should not be removed from *Penicillium* and considered as true representatives of the genus *Spicaria*. If the above considerations could be made alone this course might seem warranted. There are, however, other intergrading forms which seem to align *P. lilacinum* with the *P. janthinellum* series through *P. simplicissimum* (Oud.) Thom.

We believe the best course is to recognize the species *Spicaria violacea*,

leaving it in the genus where it was assigned by Abbott, but to call attention to the probable relationship of this form to *Penicillium lilacinum* Thom.

Spicaria violacea is a normal constituent of most soil floras. In dilution plates, upon such substrata as soil-extract-nitrate agar as used by Smith and Humfeld (1930), it appears as floccose colonies, colored in violet shades. In streak plates on hay-infusion agar (Raper, 1937), the vegetative mycelium remains submerged and the conidial structures usually develop singly and appear as masses of loose, tangled chains of essentially colorless conidia borne upon long and erect conidiophores. Not uncommonly, strains rapidly lose their capacity to produce conidia when maintained in laboratory culture.

Penicillium humuli van Beyma, in Zentbl. f. Bakt. etc., (II) **99:** 392–394, fig. 6. 1939.

Colonies on Czapek's solution agar restricted, attaining a diameter of 2.0 to 2.5 cm. in 10 days at room temperature, extremely wrinkled and buckled, especially in colony centers where the mycelial felt is often cracked on upper surfaces of folds (fig. 79A), thin, consisting of a tough basal felt characterized by a closely interlaced surface growth of trailing hyphae (described by van Beyma as "powdery"), light buff (Ridgway, Pl. XV) to pale pinkish buff (R., Pl. XXIX) in color, azonate, no exudate produced; no odor; reverse in the same shades as the colony, agar uncolored. Penicilli may appear as monoverticillate structures borne on short conidiophores, 50 to 80μ by 2.2 to 3.3μ, that arise as branches from trailing hyphae, or more complex and often conspicuously divaricate structures that may be irregularly branched but usually consist of a verticil of 2 to 3 terminal metulae and are borne on longer conidiophores up to 250μ in length that typically arise from the basal felt (fig. 79C); metulae mostly 20 to 25μ by 2.2 to 3.3μ; sterigmata usually borne in clusters of 5 to 7, mostly 10 to 15μ by 2.5 to 3.5μ (fig. 79D), producing loosely tangled chains of conidia up to 60μ long; conidia smooth, elliptical when first formed, then subglobose to globose, mostly 3.0 to 4.0μ in diameter but occasionally up to 4.5μ.

Colonies on steep agar growing more rapidly, attaining a diameter of 4.0 to 5.0 cm. in 10 days at room temperature, somewhat wrinkled in central areas, radially furrowed, heavily sporing, superficially appearing velvety but with conidial structures commonly arising as branches from ascending hyphae in darker brown shades near avellaneous (R., Pl. XL), slightly zonate; no exudate; no odor; reverse in avellaneous to fawn shades; penicilli as on Czapek except monoverticillate forms less abundant, mostly appearing as the more complex structures described above and with branch-

ing below the level of metulae common; branches usually 15 to 25μ by 2.2 to 3.3μ, with dimensions of metulae, sterigmata and conidia as above.

Colonies on malt agar spreading broadly, attaining a diameter of 6.0 to 7.0 cm. in 10 days at room temperature, plane (fig. 79B), with margin

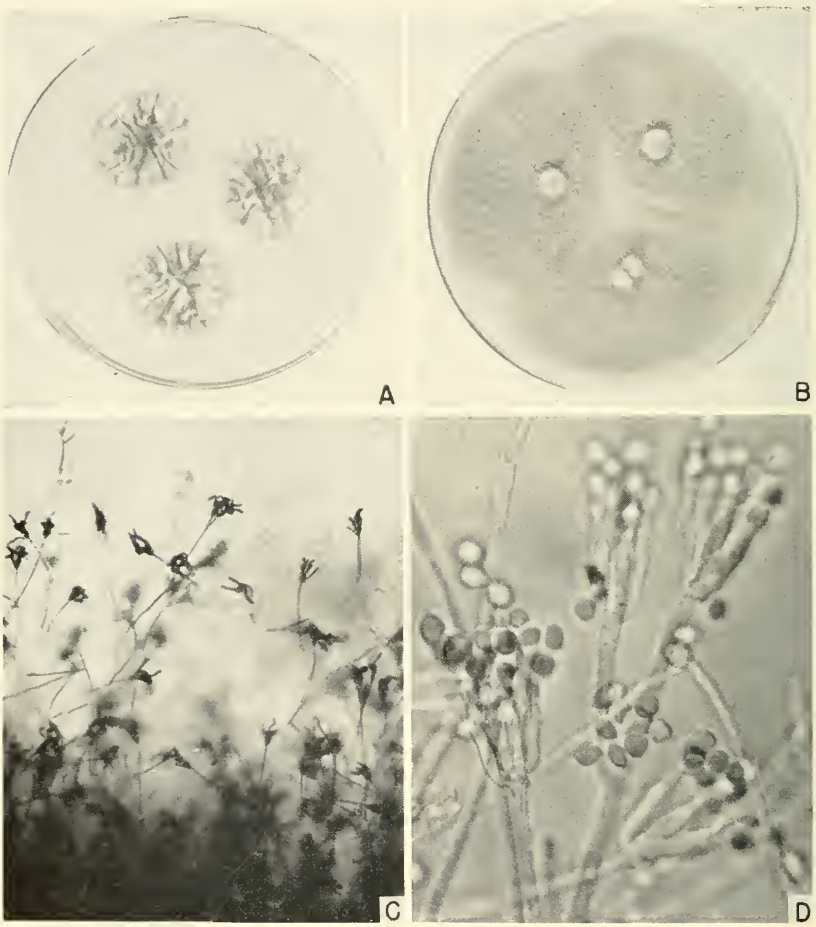


FIG. 79. *Penicillium humuli* v. Beyma, NRRL 872. *A* and *B*, Two-week-old colonies on Czapek and malt agars. *C*, Marginal colony area, × 85. *D*, Detail of penicilli, × 1000.

thin and submerged, color as above; no exudate; odor very faint; reverse in cream to light buff shades with zonation apparent; penicilli mostly the complex structures already described with an occasional monoverticillate type present.

Species description based primarily upon the type strain, NRRL 872.

This was isolated by Dr. H. Schnegg in Weihenstephan from hops, was sent to us by Westerdijk in 1938, and subsequently was described by van Beyma in 1939. A new culture of this strain has recently been received from the Centraalbureau. The two cultures duplicate one another in cultural characteristics but cellular elements of the penicilli tend to be somewhat smaller in the latter substrain and to fit van Beyma's original description better than those of NRRL 872. The identity of the two cultures, however, is unmistakable and the present description is drawn sufficiently broad to include both substrains as they now exist.

The cultures under study both stem directly from van Beyma's type but in our experience have never shown any yellow-green color such as described for the species by him. His notes were made from cultures grown on beer-wort agar and the possibility exists that coloration of colonies on this medium would differ from that upon the substrata which we have employed. This is questioned, however, since we have grown the mold upon a variety of media, including malt extract, without any suggestion of green.

Thom examined this culture prior to its description by van Beyma and suggested placing it in his Lanata-Divaricata group (1930) near *Penicillium lilacinum*. Van Beyma accepted this disposition but called attention to certain cultural features, notably the "powdery" rather than floccose surface of the colonies, which did not conform with the typical characters of this group. The validity of van Beyma's exceptions is recognized although colonies on malt tend to develop a fibrous or lightly flocculent surface. Furthermore, the penicilli commonly appear monoverticillate, or do not normally branch at a number of different levels as in *P. lilacinum*, the sterigmata are not usually characterized by pointed conidial tubes as in the latter species; and the conidia are more nearly subglobose than elliptical. Despite these differences, we believe the total cultural and morphological picture of *P. humuli* enables it to be keyed with the *P. lilacinum* series more satisfactorily than elsewhere.

Tan Mutants of Other Species

Strains which superficially resemble *Penicillium humuli* van Beyma in color and to a lesser degree in general cultural appearance, are occasionally observed as sector variants in colonies of other species. In the present study, such tan mutants have been observed in, and isolated from, normal green or blue-green colonies of both *P. spinulosum* Thom, in the Monoverticillata, and *P. rugulosum* Thom, in the Biverticillata-Symmetrica. Examination of conidial structures in both cases promptly and unmistakably confirmed their identity as mutants differing from the parents, principally in conidial color. Tan-spored cultures are occasionally iso-

lated from nature which seem to be of like origin, although definite proof is lacking. One such culture, received in July 1945 from Dr. O. G. de Lima, Recife, Brazil, approximated *P. citrinum* Thom physiologically by producing citrinin, and in morphological and cultural characteristics duplicated this species in all except conidial color. The strain is discussed elsewhere as NRRL 2145 (see p. 349).

Occurrence and Significance

Penicillium lilacinum Thom is among the most common of all soil fungi. It seems to occur regularly upon decaying vegetation in the later stages of decomposition and may be isolated less commonly from almost any type of organic substrate exposed to air-borne dust and a fairly humid atmosphere. It is very tolerant of many chemicals. Thom (1930) reported its occurrence in nickel-electrotyping baths. Lockwood (1936) isolated the species from 9 per cent sodium acetate solutions. Trabut (1895) provisionally assigned the name *P. cupricum* to a mold producing "rose-colored conidia" isolated from a 9.5 per cent solution of $CuSO_4$. The identity of Trabut's mold remains obscure, but it possibly represented a highly colored strain of *P. lilacinum*. In our experience *P. lilacinum* has been isolated from various chemicals in solution, mostly acidic, and appears to be one of the most common molds producing "bottle imps" in laboratory reagents. Heyes and Helden (1932) employed *P. lilacinum* as one of five Penicillia to test resistance of artificial silk to mold damage. Considerable "tendering" of the silk occurred prior to the appearance of any microscopically detectable injury to the fibers. Acetate silk was more resistant than other types tested. Schanderl (1942) reported *P. amethystinum* (possibly *P. lilacinum* of this Manual) as capable of assimilating atmospheric nitrogen.

Spicaria violacea occurs in nature under conditions similar to those favoring *P. lilacinum*, although apparently less commonly. No biochemical or physiological studies have been reported. *Penicillium humuli* was isolated from hops but no information was supplied regarding its possible significance in nature.

Penicillium janthinellum Series

Outstanding Characters

Colonies spreading broadly, becoming gray, gray-green, or pale bluish green in conidial areas; vegetative mycelium becoming orange, orange-red or reddish purple in some strains, in others remaining white or nearly so; surface growth varying from almost velvety to definitely floccose depending upon the strain and species, occasionally developing ropes; reverse at first colorless, and in some strains remaining so, in

others developing a succession of colors ranging from yellow or yellow-green through orange, or orange-red, to reddish or vinaceous purple.

Conidiophores arising directly from the substratum or as branches from trailing aerial hyphae, ranging from very short up to 1 mm. in length, with walls usually granular or roughened.

Penicilli variously branched and ranging from single terminal verticils of sterigmata (appearing monoverticillate) to asymmetric structures composed of an indefinite number of strongly divaricate branches and/or metulae bearing verticils of sterigmata.

Sterigmata few in the verticil, slender, and characteristically tapering abruptly to conspicuously narrowed beak-like conidial tubes.

Conidia at first definitely elliptical, usually becoming ovate to subglobose in age with one or both apices often pointed, and with walls smooth or delicately roughened.

Series Key

1′. Conidial chains strongly divergent and/or becoming tangled in age, not tending to form columns.

aa. Sterigmata abruptly tapered to narrow conidium-bearing tubes; colonies usually not funiculose ..... *P. janthinellum* series

1″. Conidia elliptical, rough with echinulations arranged in spiral or transverse bands ..... *P. daleae* Zaleski

2″. Conidia elliptical to subglobose, usually roughened but with echinulations not arranged in spiral or transverse bands.

aaa. Vegetative mycelium and colony reverse often strongly colored (orange-red, reddish purple, etc.) in new isolates *P. janthinellum* Biourge

bbb. Vegetative mycelium uncolored to light buff or peach, colonies sporulating sparingly or tardily; colony reverse colorless or in yellow to orange shades

1‴. Conidiophores conspicuously roughened; penicilli commonly consisting of a terminal verticil of divergent metulae; conidia elliptical to subglobose, finely echinulate; reverse uncolored to yellow ..... *P. simplicissimum* (Oud.) Thom

2‴. Conidiophores finely roughened; penicilli irregular; conidia elliptical, smooth or finely roughened; reverse in orange shades ..... *P. ochro-chloron* Biourge

3‴. Conidiophores smooth or nearly so; penicilli commonly irregular; conidia elliptical to subglobose, conspicuously roughened; reverse in cream to light tan shades *P. piscarium* Westling

4‴. Conidiophores smooth or nearly so; penicilli irregular; conidia subglobose to elliptical, smooth; reverse in bright yellow to yellow-orange shades ..... *P. miczynskii* Zaleski

In 1918, Thom, in Pratt's "Soil Fungi of Idaho" (Jour. Agr. Res. **13:** 94–95, figs. 3 and 4) discussed these forms under the heading "Soil Peni-

cillia." In his Monograph (1930), he referred to them as the *Penicillium janthinellum* series, a usage which we have followed since that time. The members of the series are unusually variable, individually and collectively, and it has seemed best to designate the whole aggregate by the name which he believed could be most satisfactorily applied to the general type of culture most abundant among them.

Aerial growth ranges from comparatively thin, loose-textured to floccose or floccose-funiculose in some strains. The series is characterized by its rapidly spreading and often highly pigmented colonies, by its irregular and very divergent penicilli, and especially by its sterigmata which taper abruptly to long and narrow conidium-bearing tubes. Seven species are recognized, as follows: *Penicillium daleae* Zaleski, *P. janthinellum* Biourge, *P. simplicissimum* (Oud.) Thom, *P. ochro-chloron* Biourge, *P. piscarium* Westling, *P. miczynskii* Zaleski, and *P. godlewskii* Zaleski. The first of these is distinguished particularly by the spiral banding of its conidia, and is clearly related to this series by the character of its sterigmata. The second species is by far the most abundant and the most variable. It is seldom equalled among the Penicillia in the variety of colors it displays. When first isolated, strains are commonly highly pigmented, but usually become less colorful with continued laboratory cultivation. *Penicillium simplicissimum* is often heavier sporing, shows conidiophores generally longer, and consistently fails to develop appreciable color either in the mycelium or the colony reverse. *Penicillium ochro-chloron* typically develops as white to slightly tinted colonies with limited sporulation upon all substrata; the species is noteworthy for its tolerance of copper and high acidities. *Penicillium piscarium* is a comparatively light colored, loose-textured form with elliptical and strongly echinulate conidia. It is known only as the type culture although strains approximating it are occasionally encountered. *Penicillium miczynskii* is marked by colonies at first white to flocculent, becoming light yellowish green at maturity with yellow vegetative mycelium abundantly produced. *Penicillium godlewskii* is marked by colonies generally more or less funiculose. Close relationship to the *P. janthinellum* series is doubtful, but the species can be considered adjacent to this series more conveniently than elsewhere.

Penicillium daleae Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B., pp. 495–496; Taf. 57. 1927. Thom, The Penicillia, pp. 360–361. 1930.

This species as described and illustrated by Zaleski, and as observed by Thom (1930), showed coarsely roughened conidia on which the roughness was concentrated in transversely and usually spirally arranged bands. The type strain was lost from our Collection between 1935 and 1940, and for the present study a new culture of this strain was sent by the

Centraalbureau and is now maintained by us as NRRL 2025. This latter culture no longer produces colonies conforming with Zaleski's (1927) and Thom's (1930) descriptions, nor does it produce well-developed penicilli on any culture medium employed. The conidia, however, are entirely characteristic of the species. Due to their unique markings there is no question as to the authenticity of the culture from Baarn.

Since the culture now in our possession fails to present the cultural aspect of the species as originally isolated and studied, the description presented here represents a condensation of Zaleski's original diagnosis as presented by Thom in his Monograph (1930, p. 361), followed by pertinent culture notes by the latter investigator made prior to 1930:

"Colonies in neutral Raulin with 10 per cent gelatine in petri dishes, slowly growing becoming 24 to 26 mm. in diameter in 12 days, liquefying the gelatine tardily but completely, velvety or somewhat closely subfloccose, zonate only indistinctly and in the outer area, with the whole central area thrown into broad regularly radiate wrinkles, with the very center somewhat depressed and showing a few uncolored drops; white marginal zone 2 to 3 mm. wide; in color conidial areas at first blue-green shades such as 371, 372,[1] becoming dark yellow-green shades such as 273, and later dark orange-brown such as 168, 164, 198, 139; reverse at first in orange-yellows such as 171, 166, 157, to 133, 138, later becoming red-orange 84, 88, 92, 97; odor none or weak; conidiophores 10 to 200 or 300 by 2 to 2.5μ, with apex more or less enlarged or inflated, commonly unbranched, occasionally with short branches, flexuous, varying greatly in length, erect or ascending; penicilli mostly 10 to 12μ, less frequently 25 to 30μ or 40μ long, with walls smooth; metulae 8, 10, to 20 or 24 by 2.5 to 3.0μ, in groups of 2 or 3, commonly unequal and irregularly arranged, with apices commonly inflated; sterigmata about 9 to 10 by 2.5 to 3.0μ, commonly in verticils of 3, 5 to 10 or 12, sometimes occurring singly; conidia 2.5 to 4.0μ by 2.5 to 3.0μ, varying considerably in size, coarsely denticulate, ovate elongated or subglobose.

"Habitat: Species isolated from soil under pine near Poznan, Poland."

Thom's notes follow:

"The type strain growing well at both 20° and 30°C. Colonies upon Czapek's solution agar at 20°C., spreading fairly widely (30 mm. in diameter in seven days), floccose with some funiculose or fasciculate hyphae (more deeply floccose in slanted tubes than in petri dish cultures), gray-green with white marginal areas 2 to 3 mm. in width during the growing period (at 30°C. pitted mycelial mass thinner, radiately wrinkled and wanting in green color); reverse in areas purple drab (Ridgway, Pl. XLV); drops in central area, colorless; conidia coarsely roughened with winding color bars, elliptical to subglobose 4 by 3μ."

Our current notes on NRRL 2025 follow: Colonies on Czapek's solution agar attaining a diameter of 4.0 to 4.5 cm. in 12 days to 2 weeks at room temperature (24°C.), producing a rather delicate basal felt with surface growth somewhat floccose and with marked development of funicles often apparent at the colony margin, radially furrowed, almost azonate, white

[1] Color references refer to tabs in Kleinecksieck and Valette's Code des Couleurs, Paris. 1908.

with submarginal zone becoming slightly gray with the very sparse development of conidia, no exudate produced; odor almost lacking, slightly sourish; reverse uncolored to cream; conidia generally borne upon single sterigmata or upon very small clusters of sterigmatic cells, 8 to 12μ by 2.0 to 2.5μ with abruptly narrowed apices, arising from aerial hyphae, rarely from structures suggesting true penicilli, elliptical to subglobose, 3.0 to 3.5μ by 2.5 to 3.0μ, with coarse roughenings in spirally-arranged bands or bars.

Colonies on steep agar spreading more rapidly, attaining a diameter of 6.0 to 6.5 cm. in 12 days, closer textured and more conspicuously furrowed than on Czapek but otherwise duplicating the preceding.

Colonies on malt agar spreading broadly, up to 8.0 cm. in 12 days, loose-textured, floccose, with surface growth showing a network of aerial hyphae or thin ropes of hyphae, lightly sporulating with penicilli limited in number and almost invariably monoverticillate.

In Thom's Monograph (1930), *Penicillium daleae* was placed in his Asymmetrica-Funiculosa because of the tendency of colonies to show some ropiness. Biourge had earlier placed it near to, or identical with, *P. janthinellum*. Upon re-examination of Zaleski's description and illustrations, and after re-study of the type strain, we regard the species as clearly distinct from, but closely related to, *P. janthinellum*. The penicilli, even at the time of original isolation, were much smaller than in forms such as the *P. terrestre* series, and were apparently divaricate. The vegetative hyphae are delicate, and colonies, on the whole, bear a much closer resemblance to the Divaricata than to the Funiculosa.

The species, apparently, is not common in nature, since forms with its peculiar pattern of conidial markings are rarely observed. The type isolated by Zaleski from soil under pine near Poznan, Poland, is currently maintained, in somewhat altered form, by the Centraalbureau and by the Northern Regional Research Laboratory Collection as No. 2025.

Penicillium krzemieniewskii Zaleski (in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 490–492; Taf. 56. 1927) was originally described in terms strongly suggestive of *P. daleae* Zaleski, and conidia were illustrated with echinulations in winding bands. This character was likewise emphasized by Thom in 1930, and is still clearly evident in the culture studied by him and now retained by us as NRRL 922. A culture received from the Centraalbureau in May 1946, which presumably represents Zaleski's type, has also been compared culturally and microscopically with *P. daleae* (NRRL 2025) in the current study, and the two cultures are strikingly similar, differing primarily in the slightly heavier, but still sparse, production of conidia by *P. krzemieniewskii* and the more delicate and more closely spaced roughening of its conidia. The type strains of Zaleski's two species are not identical, but they do not differ more than variant members of such well recognized species as *P. roqueforti*, *P. expansum*, etc. Since Zaleski's types are believed to represent variants of a single species, and since *P. daleae* is the more striking of the two forms, we feel that this

species should be recognized and that *P. krzemieniewskii* Zaleski should be regarded as a synonym.

Penicillium janthinellum Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 258–260; Col. Pl. VII and Pl. XII, fig. 70. 1923. See also Thom, The Penicillia, pp. 238–241. 1930; and Thom in Pratt in Jour. Agr. Res. **13:** 94–95, figs. 3 and 4. 1918.

Colonies on Czapek's solution agar (Col. Pl. V) spreading, attaining a diameter of 5 to 7 cm. in 10 days at room temperature (24°C.), forming a tough, closely interwoven felt of fine hyphae, with growing margin broad, with surface growth delicately floccose, unevenly tufted, or in some strains ropy, irregularly wrinkled in central portions and radially furrowed in marginal colony areas (fig. 81A), at first white, but in most strains becoming variously colored from the tardy and irregular development of conidial areas, mostly in pale gray to glaucous gray shades (Ridgway, Pl. XLVIII), and the simultaneous shading of non-fruiting areas to dull buff, orange-red, or in some strains purple-vinaceous shades (R., Pl. XLIV), azonate or broadly zonate; exudate usually lacking or limited, occasionally abundantly produced, colorless to amber, brownish, or vinaceous; reverse of colonies sometimes colorless, especially in stock cultures after many transfers, but usually in bright shades, in new isolates commonly yellow-green to orange at first, quickly changing to orange-red, maroon or purple-red shades; penicilli typically asymmetric, strongly divaricate with conidial chains divergent (fig. 80A) or tangled and commonly up to 200μ in length, abundantly produced in some strains, less abundantly in others, sometimes thinly or evenly distributed over the whole colony but generally more abundant in submarginal areas, borne terminally on ascending conidiophores up to 500μ in length by 3.5μ in diameter, with walls smooth or finely roughened (fig. 80B), or on short branches from aerial hyphae commonly 10 to 50μ by 2.5 to 3.0μ, varying in complexity from simple verticils of sterigmata (appearing monoverticillate) (fig. 80B_3) to verticils containing both metulae and sterigmata, or verticils of metulae of unequal length, and occasionally larger structures with metulae and sterigmata borne upon one or more branches in addition to the main axis (fig. 80B_2 and B_1); branches variable, ranging from 10 to 25μ by 3.0 to 3.3μ; metulae mostly 10 to 15μ by 2.0 to 2.5μ, but ranging from 7 to 20μ in length, with apices more or less vesiculose; sterigmata diverging, enlarged at the base then tapering abruptly to fairly long conidium-bearing tips (fig. 80B_5), mostly 8 to 10μ by 2.0 to 2.2μ; conidia strongly elliptical when formed and usually remaining elliptical, but in some strains becoming ovate to subglobose, with ends often apiculate and walls more or less roughened (fig. 80C), commonly 3.0 to 3.5μ in long axis.

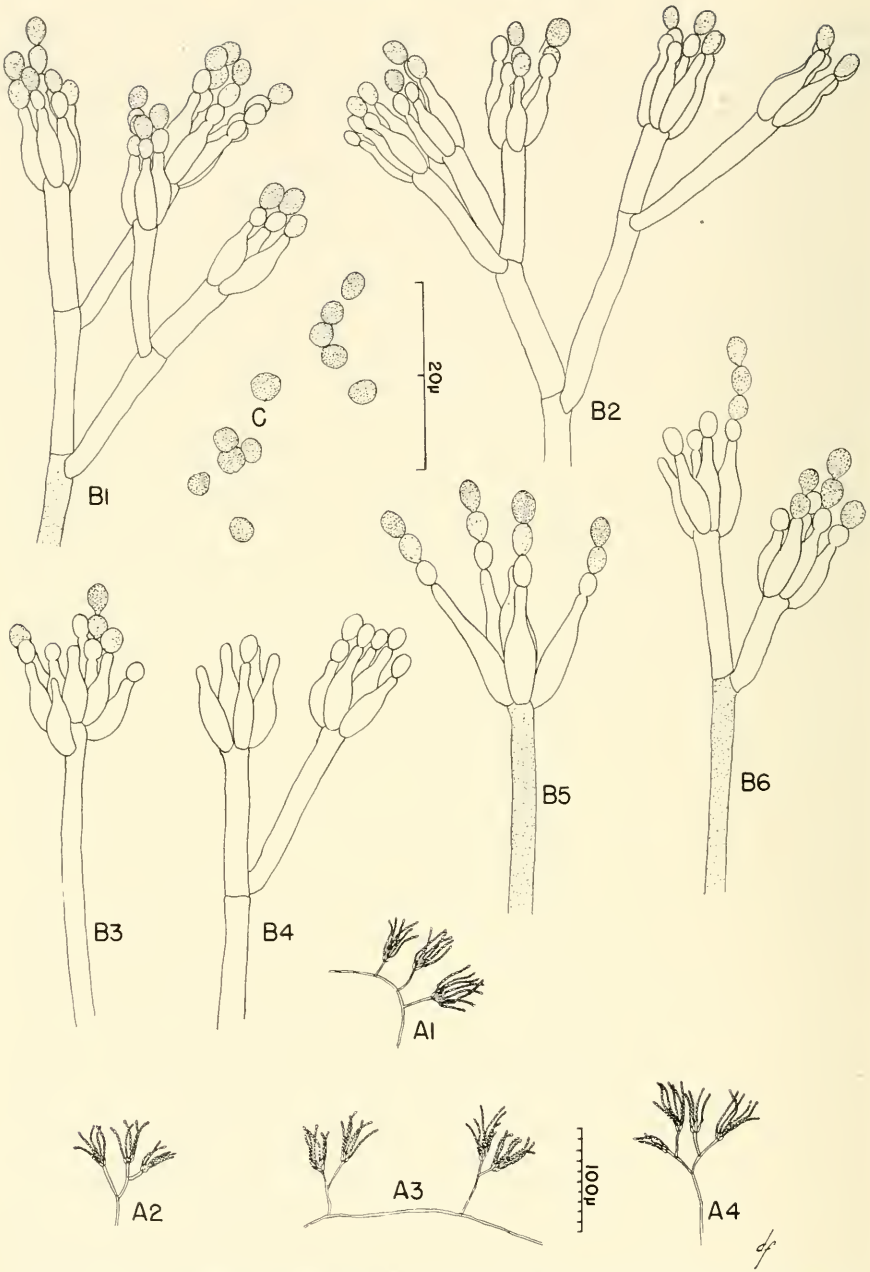


FIG. 80. *Penicillium janthinellum* Biourge. A_1–A_4, Habit sketches of representative penicilli. B_1–B_6, Penicilli showing details of structure and common variations in pattern—some conidiophores are smooth and others fairly roughened. *C*, Mature conidia, showing characteristic delicate echinulation.

Colonies on steep agar growing somewhat more rapidly than on Czapek but generally of similar texture, often more intensely colored with the shades present on Czapek more accentuated; conidial structures less commonly monoverticillate than on Czapek but otherwise conforming to the above description.

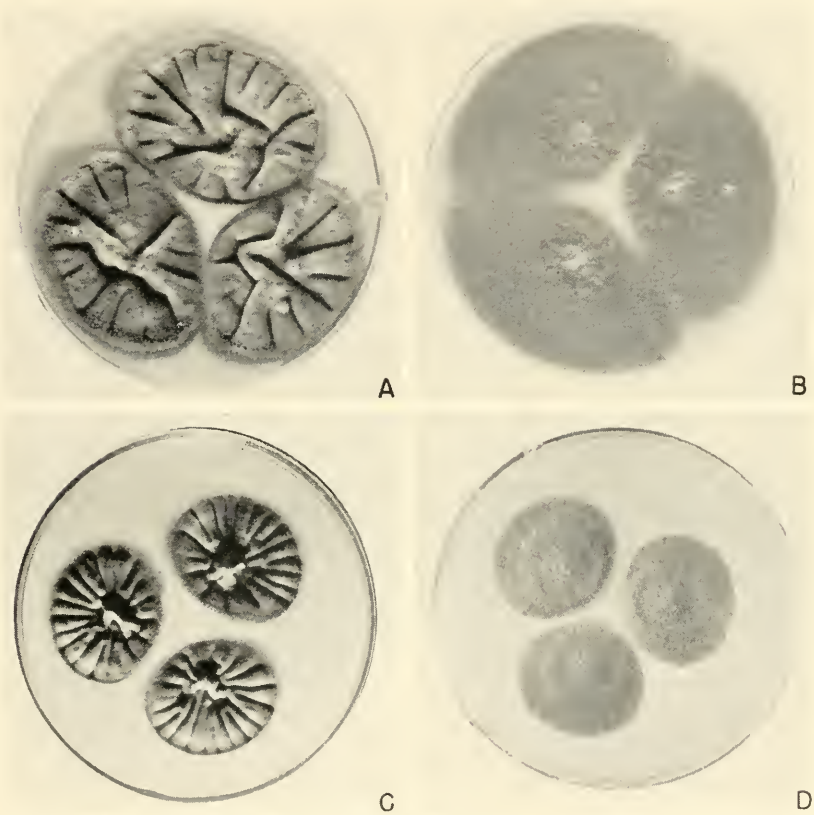


FIG. 81. *A* and *B*, *Penicillium ianthinellum* Biourge, NRRL 2016, on Czapek and malt agars at two weeks. *C* and *D*, *P. simplicissimum* (Oud.) Thom, NRRL 902, on same media, same age.

Colonies on malt agar spreading broadly, thin but of looser texture than on Czapek (fig. 81B), heavier sporing, usually in gray to glaucous gray shades, consistently lacking the colored mycelium characterizing the same strains on Czapek and steep agar; exudate not produced; reverse dull yellow-brown, never in red-purple shades; penicilli commonly larger than on Czapek but essentially similar in pattern.

Species description based primarily on Thom's description of his num-

ber 4789 as listed in his Monograph (1930, p. 341), NRRL 904 isolated from Virginia soil in 1928, NRRL 2016 isolated from Nicaragua soil in 1945, and numerous other strains now in our possession or examined in previous years.

This species is probably the most abundant *Penicillium* found in soils, having been isolated from samples world-wide in origin. It is also commonly isolated from decaying vegetation undergoing final stages of decomposition. While not so frequently isolated from fabrics or other military equipment as members of the *Penicillium citrinum* series or the *P. lutcum* series, these forms are commonly obtained from these and related sources.

In soil dilution plates, *Penicillium janthinellum* characteristically appears as a rapidly spreading, medium to light sporulating form with colony surface often orange to vinaceous in color and with reverse typically in bright orange-red to purple-red shades. When first isolated and grown in laboratory culture, individual strains usually produce this characteristic picture but, upon continued cultivation, tend to become less highly colored and to produce fewer conidial structures. After 10 or more years of continuous laboratory cultivation many strains become essentially sterile and fail to produce characteristic colors either in their vegetative mycelium or the colony reverse. NRRL 904 represents such a strain. When isolated in 1928 this strain was highly colored and was considered representative of the species; today it is almost sterile, produces colonies with vegetative hyphae cream to flesh-colored and with colony reverse ranging from peach to pale orange. However, the penicilli produced, and particularly the sterigmata, remain wholly characteristic of the species. A culture received from the Centraalbureau under this name is comparatively heavy sporing, develops a minimum of colored vegetative hyphae, and produces colonies with reverse in peach shades. The penicilli produced by it are likewise characteristic of the species. Strain NRRL 2016, noted above, is regarded as entirely typical of the species as it is understood by us. It sporulates fairly abundantly and produces colonies on Czapek and steep agars in which both the vegetative mycelium and the colony reverse are highly colored. By relying upon the lyophil technique for culture preservation (see p. 79) it is hoped that this culture may be kept in an unaltered form for many years.

Penicillium guttulosum Gilman and Abbott (Iowa State College, Jour. Sci. **1**: 298, fig. 33. 1927) was described to cover some member of the *P. janthinellum* series characterized by the production of an excessive amount of exudate. The original description was written in terms which clearly ally it with *P. janthinellum*. Since exudate production is an extremely variable character in the latter species, we regard *P. guttulosum* as representing merely an extreme variant in this abundant and diverse series.

The type culture of *P. guttulosum*, NRRL 907, as maintained in this laboratory, now produces colonies that are almost white and essentially sterile, but are still characterized by the production of very abundant exudate. A strain received from the Centraalbureau under this name and isolated by them in 1937 conforms fairly well with the original description but fails to show any marked difference from other strains diagnosed as *P. janthinellum*. In view of the great cultural variability that characterizes members of the series as isolated from nature, and in view of their tendency to become less highly colored and less heavily sporulating in continued laboratory culture, we believe *P. guttulosum* should be regarded as a synonym of *P. janthinellum*.

Penicillium glauco-roseum Demelius (Verhandl. Zool. Bot. Gesellsch. Wien. **72**: 72, fig. 3. (1922) 1923) also is believed to be synonymous with *P. janthinellum*. The original description emphasized the presence of rosy crystals and granules in the fruiting structures and the irregular character of the penicillus, the latter character being responsible for its placement in the *P. janthinellum* series by Thom in 1930. In 1928, Thom assigned to this species a strain (NRRL 908) isolated from Virginia soil. This has been maintained in culture, and when examined in the current study fails to show any distinguishing characters to separate it from *P. janthinellum*. Unlike many representatives of this series it has consistently maintained its capacity to produce colonies with reverse in bright purple-red shades. The production of rosy crystals and granules by Demelius' culture suggests a possible relationship to *P. purpurogenum* and related forms in the Biverticillata-Symmetrica. No authentic culture was obtainable and its proper placement could not be definitely established; but, if primary emphasis is placed on the character of the penicillus produced, her description would seem to require assignment with *P. janthinellum*.

Penicillium rivolii Zaleski (Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 471–473; Taf. 50. 1927) was described by Zaleski in terms which clearly ally it with *P. janthinellum* as considered by Thom in his Monograph (1930). Examination of his type strain (NRRL 906 = Thom No. 5010.20) in culture at that time confirmed this placement. However, the species was regarded as valid since the original description and Zaleski's figures were satisfied reasonably well by the type. The examination of many additional cultures belonging to the *P. janthinellum* series since that time, and more particularly during our current study, leads us to conclude that *P. rivolii* represents merely one cultural aspect of the extremely abundant species, *P. janthinellum*.

Penicillium proprium Morotchkovsky (Bul. Sci. Recueil Biol. Univ. Kiev. **2**: 78, fig. 7. 1936) is believed to represent some member of the *P. janthinellum* series. The author's description follows: Colonies round, woolly or floccose, radiately wrinkled, at first cream white, at length gray; reverse uncolored or yellowish; conidiophores slender, unseptate, 350 to 400 by 1.5 to 2.7μ; creeping, arising from a floccose mass, simple or producing two or three divaricate branchlets or metulae at the apex; metulae 10.5 to 13.6 by 1.8 to 2.5μ; sterigmata in two's, three's or four's, sharp pointed at the apex of the branchlets or sometimes arising directly from the conidiophore below the apex; 6.0 to 8.0 by 1.5 to 2.0μ; conidia globose, 1.8 to 2.5μ in diameter, smooth or scarcely noticeably punctulate, in chains showing connectives; coremia none; odor slightly moldy. Habitat: In rotting sugar beet roots, 1929. The culture has not been seen by us. Comment: The description with the divaricate character of the penicillus as shown in his figures and with the sharp pointed sterigmata would put this close to the *P. janthinellum* series.

Penicillium simplicissimum (Oud.) Thom, in The Penicillia, pp. 335-336, fig. 51. 1930.

Synonym: *Spicaria simplicissima* Oudemans, in Nederl. Kruidk. Arch. ser. 3, **2:** 763. 1903. See also Jensen, Cornell Agr. Exp. Sta. Bul. 315, p. 493, fig. 127. 1912.

Colonies on Czapek's solution agar attaining a diameter of 4.0 to 4.5 cm. in 12 to 14 days at 24°C., 0.5 to 1.0 mm. deep (fig. 81C), with surface growth loose to almost velvety, composed of a network of trailing and branching hyphae borne upon a tough basal felt, at first white, but later developing abundant conidial heads and becoming pale blue-green near light celandine to artemisia green (Ridgway, Pl. XLVII) in marginal and submarginal areas with the ripening of conidial structures, central colony area often somewhat raised and submarginal areas marked by more or less well-developed radial furrows; azonate or slightly zonate in some strains; vegetative hyphae thin, rarely exceeding 2.0μ in diameter, uncolored; exudate limited to abundant, colorless; odor lacking or indefinite; colony reverse colorless or in yellow shades, in some strains approximating straw to amber yellow (R., Pl. XVI). Penicilli usually not abundantly produced, fairly late in developing and mostly concentrated in a narrow to relatively broad marginal zone, asymmetric, strongly divaricate, rarely showing true branches but commonly consisting of more or less well-defined terminal clusters of 2 to 4 divergent metulae bearing verticils of sterigmata (appearing essentially monoverticillate), and borne upon ascending conidiophores arising mostly from the substratum, or smaller structures consisting of verticils of sterigmata only, borne upon short conidiophores arising from vegetative hyphae or upon side branches at lower levels on the ascending conidiophores; penicilli characterized by long, divergent to loosely-tangled chains of conidia; conidiophores with walls roughened, varying greatly in dimensions, ranging from 200 to 800μ or longer by 2.5 to 3.0μ in larger structures, to very short, commonly less than 50μ by 2.5μ, when arising as lateral branches; metulae variable and often unsatisfactorily identifiable, mostly 12 to 18μ by about 2.5μ, but showing a range from 10 to 25μ by 2.5 to 3.0μ; sterigmata mostly in clusters of 4 to 10, measuring 8 to 10μ in length and 2.0 to 2.5μ wide in basal portion, tapering abruptly to a conspicuous, narrow conidium-producing tube about 2.0 to 2.5μ by 1.0μ; conidia at first strongly elliptical, usually remaining so but not infrequently appearing subglobose, mostly 2.5 to 3.0μ in long axis with walls finely echinulate.

Colonies on steep agar growing more rapidly than on Czapek, attaining a diameter of 5.5 to 6.0 cm. in 10 to 12 days, heavily sporulating in central colony areas, conspicuously zonate and with successively older areas rang-

ing from light celandine green at colony margin, through celandine green to mineral gray (R., Pl. XLVII) to olive gray or even deep olive gray (R., Pl. LI) in colony center; radial furrows more strongly developed; limited colorless exudate produced; odor lacking or indefinite; reverse colorless to dull yellow; penicilli generally larger than on Czapek, consisting of a greater number of monoverticillate-like structures, and with conidial chains even longer and more divergent; arrangement and measurements of metulae and sterigmata as on Czapek.

Colonies on malt agar spreading, in some strains completely covering the plate in 10 to 12 days, in others attaining a diameter of 5 to 6 cm., plane, heavily sporulating throughout, almost velvety (fig. 81D), gnaphalium green to celandine green (R., Pl. XLVII); no exudate produced; reverse in dull yellow shades or occasionally appearing purplish; penicilli as described above except that metulae are more consistently clustered in true biverticillate fashion; conidiophores and metulae with walls roughened and with contents appearing vacuolate.

Species description centered upon culture NRRL 902, received in 1940 from Mrs. E. M. Laughton, Cape Province, South Africa, as an isolate from a flannel bag; and additional cultures, mostly isolated from deteriorating fabrics, contributed by various collaborators. The species as here described seems to be associated most commonly with the deterioration of textile products under field conditions, but the form should be considered as typically a soil organism that might be expected to occur wherever mixed contamination occurs and conditions favor its development.

Penicillium ochro-chloron Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 269–270; Col. Pl. X and Pl. XVII, fig. 100. 1923. Also Thom, The Penicillia, pp. 363–364. 1930.

Colonies on Czapek's solution agar growing rather rapidly, attaining a diameter of 4.0 to 5.0 cm. in 12 to 14 days at room temperature (25°C.), consisting of a closely interwoven basal felt of fine vegetative hyphae with surface somewhat floccose and cottony (fig. 82A), 0.5 to 1.0+ mm. deep, showing trailing hyphae or thin ropes of hyphae, at first near pure white but becoming slightly tinted after 8 to 10 days and at two weeks commonly approximating cartridge buff (Ridgway, Pl. XXX) or even showing light flesh shades, with central colony areas commonly depressed and with outer areas sometimes showing broad shallow radial furrows, azonate or in some cases becoming zonate with the more abundant development of conidial structures in submarginal areas; conidial structures usually produced in limited numbers, often hardly affecting the overall appearance of the colony; exudate produced abundantly in some strains, not in others, colorless; odor lacking or slightly sourish; reverse in buff to flesh colors with

submarginal zones often more intensely yellow-orange in color; penicilli fairly abundant in some strains, less abundant in others, but always more concentrated in marginal than central colony areas, variable in size and in complexity, strongly divaricate with conidial chains divergent and often tangled in age, not tending to adhere into columns; conidiophores variable in length, often arising as branches from aerial hyphae and rarely exceed-

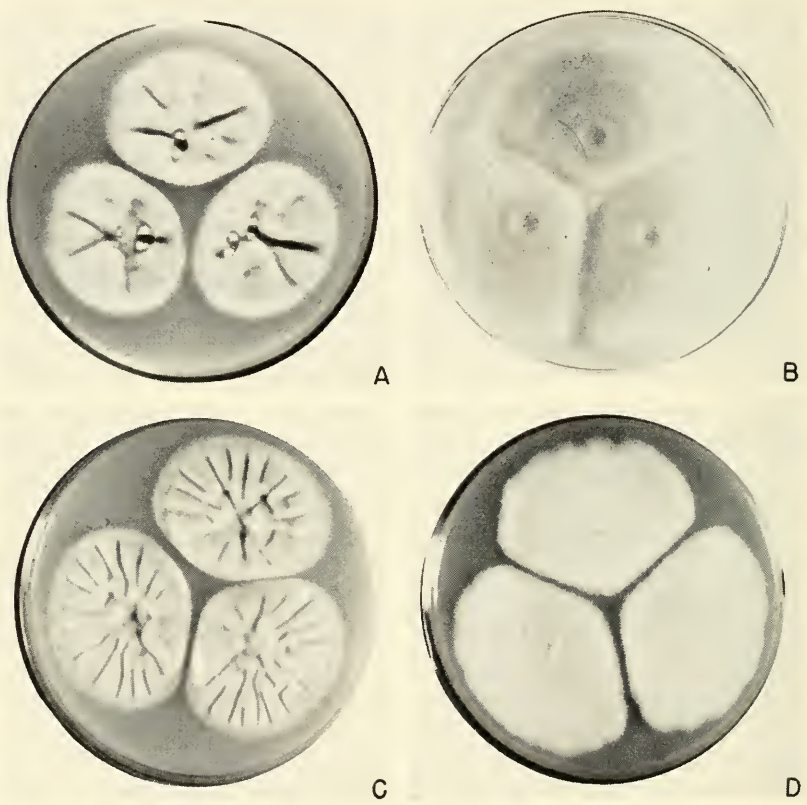


FIG. 82. *A* and *B*, *Penicillium ochro-chloron* Biourge, NRRL 927, on Czapek and malt agars at two weeks. *C* and *D*, *P. piscarium* Westling, NRRL 1075, on same media, same age.

ing 100μ by 2 to 2.5μ, less commonly arising from the substratum, up to 300 to 500μ in length by 2.0 to 2.5μ or 3.0μ in diameter, with walls finely but conspicuously roughened; fruiting structures appearing variously monoverticillate, irregularly and unequally branched, or occasionally with fairly well defined terminal verticils of 2, 3, or 4 metulae, or branches, but with the identity of such structures (whether metulae or branches)

often difficult to establish, variable in size from 10 to 20μ by 2.0 to 2.5μ with walls commonly rough; sterigmata borne in groups of 3 to 10, usually compactly arranged but with apices divergent, about 7.5 to 8.5 by 2.0μ, with basal portion about 6.0μ in length, then narrowed abruptly to form a slender conidium-bearing tube, 1μ or less in diameter; conidia elliptical, with one end commonly apiculate, mostly 3.0 to 3.5μ by 2.0 to 2.5μ, with walls smooth or very delicately roughened.

Colonies on steep agar spreading broadly, 7.0 to 7.5 cm. in 12 to 14 days at 25°C., in texture essentially as on Czapek but showing a greater diversity of color, with central colony areas predominantly sterile and approximately tilleul-buff (R., Pl. XL), ranging to court gray or mineral gray (R., Pl. XLVII) in submarginal areas where conidial structures are more abundantly produced; exudate limited in amount, colorless to pale straw color; odor lacking or indefinite; reverse in dull, dirty orange shades; penicilli similar in pattern but more abundantly produced and consistently larger than on Czapek, with conidial chains tangled, often more than 100μ in length.

Colonies on malt extract agar spreading broadly, commonly covering the entire culture plate (9 cm. ±) in 12 to 14 days, in some strains sporulating lightly, approximating court gray (R., Pl. XLVII) and appearing loosely floccose (fig. 82B), 2 to 3 mm. deep, in other strains sporulating abundantly, approximating light pea green (R., Pl. XLVII), appearing almost velvety to the naked eye but showing a surface network of aerial hyphae and thin ropes of hyphae when examined under low powers; reverse in dull orange shades; no exudate or odor; penicilli essentially as on steep agar but more abundantly produced and with walls more coarsely roughened.

Species description centered upon NRRL 926 received from Professor Hotson, University of Washington, Seattle, from a two percent solution of copper sulphate. Duplicated also by NRRL 927, received from C. L. Bedford, University of California as a copper sulphate-tolerant mold; NRRL 924 received from Dr. K. Sakaguchi, Tokyo Imperial University as the type strain of *Penicillium cuprophilum* Sato, also copper tolerant and capable of growing in high concentrations of copper sulphate and sulphuric acid (this differs from the above in producing more restricted colonies on malt); NRRL 925 received from Sakaguchi as *P. biforme* var. *vitriolum* Sato, likewise copper tolerant and capable of growing in high concentrations of sulphuric acid and in solution of copper sulphate up to 21 percent (1939), duplicates almost exactly cultures NRRL 926 and 927.

The repeated isolation of this species from copper solutions can hardly be regarded as a coincidence. We are led to presume that we are dealing with a form characterized by an unusual tolerance of this metal. *Peni-*

cillium ochro-chloron is not infrequently isolated from tentage and fabrics treated with copper naphthanate or other copper-bearing mildewcides. Despite its apparent selectivity, the species should probably be regarded, like other members of the *P. janthinellum* series, as basically a soil form

Penicillium cuprophilum Sato (Jour. Agr. Chem. Soc. Japan **15:** 359–369, illust.; and Bul. Agr. Chem. Soc. Japan **15:** 77. 1939 (in English)) was described as follows: Colonies in Czapek's solution agar in the scarcely zonate group, floccose with marginal area consisting of a deep floccose mass of mycelium, 6 mm. deep and 5.4 to 5.0 cm. in diameter after 10 days; central mass greenish glaucous with ripening conidia, then turning to olive-buff, and finally to light mineral gray, with reverse ochraceus-orange. Drops abundant, colorless or on Koji extract agar orange-yellow. Conidiophores 20 to 200μ by 2 to 3μ, smooth-walled, and asymmetrically branched; branches 15 to 20μ long; metulae 12 to 17μ by 2 to 3μ, 1 to 3 in group. Sterigmata about 7 to 8μ by 1.0 to 1.5μ, in verticils of about 1 to 5. Conidia globose or elliptical 2 to 3μ by 1.5 to 2.5μ smooth; conidial chains tangled. Hyphae 3μ in diameter, smooth. In the presence of $CuSO_4$ the older hyphae show great distortion. The type received from Sakaguchi proved to be a fairly typical strain of *P. ochro-chloron* Biourge, with which species we regard it as synonymous.

Penicillium biforme var. *vitriolum* Sato (Jour. Agr. Chem. Soc. Japan **15:** 359–369, illust. and Bul. Agr. Chem. Soc. **15:** 76–77 (in English). 1939) was described as follows: Colonies on Czapek's solution agar 7 mm. deep, 7 cm. in diameter in 10 days, gelatine not liquefied, floccose, zonate, first white then central areas dark bluish glaucous with ripening conidia, changing to olive-buff, vinaceous buff finally to light grayish olive. Reverse warm buff. Drops abundant. Odor none. Conidiophores with smooth walls about 20 to 140μ by 2 to 3μ, asymmetrically branched; branches 15 to 25μ long; metulae 12 to 20μ by 2 to 3μ, 2 to 3 in group; sterigmata about 10 to 12μ by 2.5 to 3.0μ in verticils of 1 to 5; conidia globose or elliptical 2 to 4μ by 1.5 to 3.5μ smooth. Conidial chains tangled. Hyphae 3μ in diameter, smooth-walled. In the presence of 21 per cent $CuSO_4$ the older hyphae show great distortion. Grows vegetatively but does not sporulate at 21 per cent $CuSO_4$. The type received from Sakaguchi represented a typical strain of *P. ochro-chloron* Biourge, with which we regard it as synonymous.

Penicillium piscarium Westling, in Arkiv för Botanik **11:** 54, 86–88, figs. 13 and 55. 1911; see also Biourge, Monograph, La Cellule **33:** 190–191, Col. Pl. XI, fig. 2 and Pl. XVIII, fig. 107. 1923; and Thom, The Penicillia, pp. 487–488, fig. 85. 1930.

Colonies upon Czapek's solution agar spreading, attaining a diameter of 5.0 to 6.0 cm. in 12 to 14 days at room temperature, white or slightly colored in shades near light grayish olive (Ridgway, Pl. XLVI), zonate, more or less radially furrowed (fig. 82C), commonly raised in central area, consisting of a fairly tough basal felt with loose floccose surface growth 1 to 2 mm. deep, margins thin, conidial structures very sparsely produced; exudate lacking or very limited in amount; odor absent or only faintly moldy; reverse cream or in very light yellow shades; conidiophores smooth,

usually arising as short branches from aerial hyphae, 50μ or less in length by 2.2 to 3.3μ in diameter, or with penicilli borne terminally on long trailing hyphae; penicilli extremely irregular in pattern with identity of parts difficult to determine, ranging from monoverticillate or fractional, through verticils of 3 or 4 uneven branches or metulae to very complex structures with metulae and sterigmata borne at various levels on branches of unequal length, metulae producing clusters of few sterigmata or growing out into septate hyphae and usually producing a single sterigmata at the hyphal tip; conidia elliptical or ovate, 3.0 to 3.5 by 2.2 to 2.8μ, conspicuously echinulate.

Colonies on steep agar as on Czapek in rate of growth and general colony texture but lacking the raised central area, somewhat deeper—up to 3 mm., medium to fairly heavily sporing in shades near light to deep grayish olive (R., Pl. XLVI); exudate lacking or limited; odor rather sharp, ammoniacal; reverse in dull creamy yellow to pale buff shades; pattern of penicilli somewhat more regular than above, but with numbers of parts very variable; branches from 12 to 20 or even 30μ by 2.5 to 3.0μ; metulae 8 to 15μ by 2.2 to 2.8μ; sterigmata 8 to 12μ by 2.0 to 2.5μ, abruptly tapered to form narrow conidium-bearing tubes not uncommonly 3 to 4μ long; conidia as described above.

Colonies on malt agar spreading, 6.0 to 7.0 cm. in 12 to 14 days, plane, in some strains white, floccose 1 to 2 mm. deep and practically non-sporulating (fig. 82D); in others almost velvety and heavily sporing in shades near slate olive (R., Pl. XLVII); exudate and odor lacking; reverse in dull creamy yellow to yellow buff shades; conidiophores sometimes encrusted, usually longer than on Czapek, ranging from 50 to 100μ in length when borne as branches and with trailing hyphae more often terminating in conidial structures; penicilli as described above.

Species description centered upon three cultures—all presumably descended from Westling's type—namely: NRRL 1075 (Thom's No. 2549) received in 1911 from Westling; NRRL 1076 (Thom's No. 4733.97) received in 1924 from Biourge as his No. 376 which Thom had earlier sent to him as No. 2549; and NRRL 2132, received from the Centraalbureau in July 1946, as their strain of *Penicillium piscarium* obtained from Thom in 1930. The species is approximated by NRRL 2022, isolated from a piece of untreated cotton duck at Beltsville, Maryland, by P. B. Marsh.

Penicillium miczynskii Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B., pp. 482–484, Taf. 46 and 53. 1927; also Thom, The Penicillia, pp. 488–489. 1930.

Colonies on Czapek's solution agar growing restrictedly, attaining a diameter of 3.0 to 3.5 cm. in 2 weeks at room temperature, azonate or be-

coming zonate in marginal area with the development of conidial structures, irregularly raised and commonly buckled and wrinkled in a cerebriform pattern especially in colony centers, with radial furrows extending to the margins (fig. 83A), consisting of a fairly thin and brittle basal felt of white to yellow mycelium near sea foam yellow or sea foam green (Ridgway, Pl. XXXI), with surface growth close-textured or, in some strains,

FIG. 83. *A* and *B*, *Penicillium miczynskii* Zaleski, NRRL 1077, on Czapek and malt agars at two weeks. *C* and *D*, *P. godlewskii* Zaleski, NRRL 2111, on same media, same age.

becoming floccose at the colony margins, conidial structures sparingly produced over the entire colony surface but occasionally more concentrated in a narrow marginal zone, in gray-green shades near mineral gray or gnaphalium green (R., Pl. XLVII); exudate fairly abundant, in small droplets, clear or in pale yellow shades; odor faint; reverse bright yellow to yellow-orange with surrounding agar colored in lighter tints of the same

shades; conidiophores arising primarily from the basal felt, less commonly from aerial hyphae, up to 300 to 400μ by 2.0 to 2.5μ, sometimes branched, with walls smooth; penicilli variable in pattern, typically divaricate, sometimes monoverticillate or once-branched, but commonly consisting of a verticil of 3 to 5 metulae often irregular in length and sometimes arising at different levels, with sterigmata and metulae occasionally borne at the same node; metulae 8 to 15μ by about 2.0 to 2.2μ; sterigmata in fairly compact clusters of 5 to 8, measuring about 7.0 to 9.0μ by 1.5 to 2.0μ with conidium-bearing tips narrow and rather gradually tapered; conidia subglobose to elliptical, 2.5 to 3.0μ by 2.0 to 2.5μ, with walls thin and smooth or nearly so, borne in tangled chains up to 50 or 75μ in length.

Colonies on steep agar growing somewhat more rapidly, 3.5 to 4.0 cm. in 2 weeks with general appearance and texture as on Czapek but somewhat deeper, up to 1 mm. or more, radially furrowed and medium to heavy sporing, in gray-green shades near mineral gray to gnaphalium green (R., Pl. XLVII) becoming light olive gray to olive gray in age (R., Pl. LI); exudate less abundant than on Czapek; odor faint, rather pleasant; reverse and agar as described above, conidial structures as above but usually borne on longer conidiophores commonly 400 to 500μ but up to 1 mm. in length; chains of conidia tangled, with divaricate character masked when viewed dry.

Colonies on malt agar 3.5 to 4.0 cm. in 2 weeks (fig. 83B), with basal felt thin and tearing easily, or somewhat heavier and rather brittle, plane in a wide marginal area, radially furrowed at center, medium to heavily sporing, gnaphalium to pea green (R., Pl. XLVII); exudate lacking; odor faint; reverse in orange or dull yellow buff shades; conidial structure as described on Czapek.

Species description based upon Zaleski's type received in 1928 from the Centraalbureau and now maintained in our collection as NRRL 1077; duplicated by a culture of similar origin received from the Centraalbureau in June 1946, as *P. miczynskii* Zaleski.

The species is also represented by NRRL 1024, received from Biourge in 1924 as *Penicillium sulfureum* Sopp and discussed by Thom in his Monograph (1930, p. 451) under this name as No. 4733.120.

The species is approximated by a culture, NRRL 2133, received from the Centraalbureau in July 1946, as *Penicillium sulfureum* Sopp, which they obtained from Biourge in 1929. Presumably, this culture, now maintained as NRRL 2133, is derived from the same original stock as NRRL 1024. It currently differs from the latter in producing small aggregates of heavy-walled inflated cells that simulate the soft sclerotia which characterize *P. soppi* Zaleski (see p. 279). Such structures, however, were observed by Thom (1930) in his culture No. 4733.120, and were noted in his

discussion of Biourge's treatment (1923) of *P. sulfureum* Sopp. It is our belief that Zaleski's *P. miczynskii* and Biourge's conception of Sopp's species were based upon essentially similar molds. Sopp's *P. sulfureum* is believed to have represented a form approximating *P. purpurogenum* Stoll.

Another culture, NRRL 2134, received from the Centraalbureau in June 1946, as *Penicillium mangini* Duché and Heim, duplicates almost exactly that received from them in July as *P. sulfureum* Sopp. This culture was received originally from Duché in 1931 and presumably represented their type. The culture received by us was submitted to Duché when he visited our Laboratory in December 1946, but he failed to verify it as satisfactorily representing his species, maintaining that the culture studied and described by them produced larger sclerotia predominantly in light brown shades.

The presence of aggregates of inflated, heavy-walled cells in strains which otherwise closely approximate *Penicillium miczynskii*, is believed to indicate a relationship of this species to *P. soppi* in the *P. raistrickii* series. *Penicillium miczynskii* is accordingly keyed in that portion of the Divaricata also.

Penicillium godlewskii Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B., pp. 466–467, Taf. 45 and 49. 1927. Thom, The Penicillia, pp. 365–366. 1930.

Colonies on Czapek's solution agar growing rather restrictedly, attaining a diameter of 2.5 to 3.0 cm. in 2 to 3 weeks at room temperature, consisting of a fairly thin tough felt, strongly folded and wrinkled, irregularly in central area and more or less radially toward the colony margin (fig. 83C), predominantly white but in some cultures developing abundant conidial structures in marginal areas, in light blue-green shades near celandine to artemisia green (Ridgway, Pl. XLVII), in other cultures appearing "wet", definitely funiculose and producing few conidia; odor indefinite or lacking; exudate limited in amount, colorless; reverse colorless to faint yellowish; penicilli varying greatly in size and pattern but typically divaricate; conidiophores variable in size and origin, from 50 to 300μ in length by 1.5 to 2.2μ in diameter, arising either directly from the substratum or as branches from aerial hyphae, with walls smooth; penicilli consisting of single verticils of sterigmata or irregular verticils of 2 to several divergent unequal branches (metulae) about 10 to 15μ in length, some shorter about 7 or 8μ, bearing strongly divergent sterigmata and conidial chains; sterigmata mostly in clusters of 5 to 7, occasionally up to 10, typically 6 to 7μ by 2.0 to 2.2μ but very commonly swollen and up to 4.0

to 4.5μ in diameter; conidia globose to subglobose, 2.0 to 2.5μ in diameter with walls smooth or nearly so, olive-green in mass.

Colonies on steep agar growing as on Czapek but more closely wrinkled and with ropiness usually prominent, fairly heavy sporing throughout, at first pale blue-green as above, in age becoming smoke gray or light grayish olive (R., Pl. XLVI); exudate lacking; odor indefinite; reverse uncolored or in light yellowish shades; penicilli as described above.

Colonies on malt extract agar growing more rapidly, up to 4.0 to 5.0 cm. in 2 to 3 weeks at room temperature, thin, plane except in limited central area (fig. 83D), with broad margin 6 to 8 mm. largely submerged, medium sporing throughout, conidial structures commonly smaller than above and arising from the substratum or borne on trailing hyphae or limited ropes of hyphae; reverse in yellow shades with surrounding agar similarly colored.

Species description centered upon the type strain, NRRL 2111, received from the Centraalbureau in April 1946, and upon Thom's notes made upon the same type prior to 1930 and reported in his Monograph (p. 366). Strains approximating this species are not infrequently encountered in soil population studies. They commonly developed as wet, sodden, more or less bristly to funiculose colonies and characteristically produce a limited crop of conidia. They are rather difficult to maintain in culture.

A culture received from the Centraalbureau in August 1946 as *Penicillium umbonatum* Sopp, from Biourge in 1933, fails to satisfy the description of that species, but approximates *P. godlewskii* closely enough to be considered here.

The correct placement of *Penicillium godlewskii* is open to question. The divaricate character of its fruiting structures warrant placement near this point although it cannot be satisfactorily assigned to any well-defined series in the Divaricata. It is distinct from the *P. janthinellum* series in the character of its sterigmata and its general cultural habit. It cannot be keyed satisfactorily with *P. canescens* and other species adjacent to it since it shows no tendency to develop columns of conidia. It is excluded from the *P. nigricans* series by its blue-green color and by its smooth-walled conidia. Thom (1930) regarded this species as belonging in his section Asymmetrica-Funiculosa because of the funiculose habit of its aerial growth. Continued study of this character over a period of years has rendered it of doubtful value in this connection, since almost any member of the Divaricata may show this in varying degree when colonies tend to be wet or otherwise appear unhealthy.

Weighing the above considerations, we believe that the species can be best keyed adjacent to the *Penicillium janthinellum* series although it is

not included therein for the reasons listed above. The species could possibly be treated most satisfactorily as separate from any of the well-recognized series but we refrain from this course since it would accord to it a degree of recognition which we believe unwarranted.

Penicillium intricatum Thom (U. S. Dept. of Agr., Bur. Anim. Ind., Bul. 118, 75–76, fig. 31. 1910) is regarded as having approximated the type of organisms now included in *P. godlewskii*. In his original description, and in the presentation of this species in his Monograph (1930), Thom stressed its funiculose habit. Examination of additional cultures during recent years leads us to believe that the species was based upon a strain approximating our present concept of *P. godlewskii*, but showing distinctive cultural characteristics. No authentic culture was available for the current study.

Occurrence and Significance

Members of this series occur most abundantly in soil. They are also found upon vegetation in the later stages of decay, and were commonly isolated from fabrics, optical instruments, and other items of military equipment undergoing deterioration, particularly in tropical to subtropical areas, during World War II. In soil dilution platings, *Penicillium janthinellum* constitutes one of the most numerous and one of the most colorful species encountered. Under similar circumstances *P. simplicissimum* and *P. godlewskii* are isolated less frequently, whereas other members of the series may be observed occasionally. From their numbers and distribution we believe the series may be assumed to play an active role in decomposition processes.

Mallman and Michael (1940) reported *Penicillium janthinellum* and *P. ochro-chloron* to be among the Penicillia most commonly isolated from the interior of cold storage eggs. Invasion from the containers and fillers was suspected, and treatments of these with chlorophenols, particularly sodium pentachlorophenol, reduced the damage materially without imparting an objectionable odor or taste to the eggs stored therein. Morotchkovsky (1936) described a new species, *P. proprium*, believed to represent a member of this series, as an isolate from stored sugar beet roots. Graham and Greenberg (1939) reported salicylic aldehyde, when added to soil, as predisposing wheat to infection by *Pythium arrhenomanes* Drechs. and found *Actinomyces erythropolis* and a *Penicillium*, identified as probably *P. rivolii*, (see p. 303), to destroy the aldehyde, thus favoring wheat growth. Birkinshaw *et al.* (1931) reported *P. daleae* to produce some kojic acid, though less than members of the *Aspergillus flavus-oryzae* group. A variety of carbon sources were employed as substrates.

Penicillium ochro-chloron is unusually tolerant of both high acidities and metallic ions, particularly copper. Bedford (1936) reported *Penicillium* sp. (subsequently identified by Thom as *P. ochro-chloron*) to grow

in Fehling's solution containing 1.64 percent copper and to tolerate, with some distortions of the hyphae, concentrations of $CuSO_4$ up to a saturated solution. Mycelia, when ashed, were found to contain up to 1600 p.p.m. of Cu, the amount increasing with that in the medium in lower but not in higher concentrations. Other copper salts, including CuCl and $Cu(No_3)_2 \cdot 3H_2O$, were somewhat more toxic. Subsequent to this, Sato (1939) described two Penicillia, *P. cuprophilum* n. sp. and *P. biforme* var. *vitriolum* n. var., isolated from solutions containing high concentrations of H_2SO_4 and $CuSO_4$ respectively. The former was reported to grow in a 19 percent solution of $CuSO_4$ whereas the latter would tolerate 21 percent $CuSO_4$. The cultures were sent to us by Sakaguchi and both proved to be representative strains of *P. ochro-chloron*. Additional strains of the same species have been isolated from copper solutions and from fabrics impregnated with copper-containing mildewcides by other investigators and submitted to us for identification.

Chrzaszcz and Tiukow (1929) investigated acid production in species of *Penicillium* now assigned to the *P. janthinellum* series.

Kunitz (1938) reported the production of a powerful kinase, changing trypsinogen to trypsin by an unidentified strain of *Penicillium*. When subsequently studied by Thom the culture proved to be *Penicillium janthinellum* or some closely related form.

Penicillium canescens Series

Outstanding Characters

Colonies growing somewhat restrictedly upon most substrata, consisting of a fairly compact basal felt with surface growth loose-textured to more or less floccose, conidial areas in light yellow-green to gray-green shades, reverse variable, from dull peach to orange-brown or orange-red depending upon the species.

Conidiophores variable in origin and dimensions, arising either from the substratum up to 400–500μ in length, and bearing metulae irregularly disposed or in fairly well defined terminal verticils; or borne as short branches from aerial hyphae, generally much shorter, and bearing smaller and more irregular penicilli.

Penicilli conspicuously divaricate, with conidial chains typically adherent in loose divergeng columns.

Conidia globose to subglobose, with walls variable from smooth in some forms to definitely roughened in others.

Series Key

2′. Conidial chains tending to form columns, at least in young cultures; conidia globose to subglobose, somewhat roughened.....*P. canescens* series

aa. Colony reverse developing deep red or brown shades; penicilli strongly divaricate, not tending toward ramigenous.

1″. Colonies 500 to 1000μ deep, with surface growth loose, more or less floccose; conidial areas in dull blue-green shades; conidia about 2.0 to 2.5μ; reverse orange, becoming rich brown in age.....*P. canescens* Sopp

2″. Colonies deeply floccose, 2 to 3 mm. deep; conidial areas in brighter greenish glaucous shades; conidia about 3.2 to 3.6μ; reverse in deep red shades near maroon.....*P. nalgiovensis* Laxa

bb. Colony reverse uncolored or in dull peach shades, not developing dark colors; penicilli often appearing somewhat ramigenous.....*P. jenseni* Zaleski

The so-called *Penicillium canescens* series is probably artificial in character, and is proposed principally to cover species in which the divaricate penicillus is well marked, but which do not fit very satisfactorily into any other recognized series. A limited degree of relationship is believed to exist between the species represented here. All tend to produce conidial chains in loose columns, all produce long conidiophores (in part), often with fairly well organized terminal penicilli, and all produce globose to subglobose spores. Three species are included, each of which seems to be more or less intermediate between the Divaricata and some other section of the genus. *Penicillium canescens* Sopp appears to be transitional between the *P. janthinellum* and *P. nigricans* series. *Penicillium jenseni* often produces comparatively small penicilli that are somewhat ramigenous and suggests a relationship to the Monoverticillata on the one hand, or to the *P. citrinum* series through *P. corylophilum* Dierckx (see p. 341) on the other. *Penicillium nalgiovensis* Laxa, in colony texture and coloration and in details of structure, possesses characteristics which indicate affinities with certain species assigned to the Lanata or Fasciculata.

Penicillium canescens Sopp, in Monogr. pp. 181–182, Taf. XIX, fig. 136; Taf. XXIII, fig. 28. 1912. Thom, The Penicillia, pp. 347–348. 1930.

Colonies on Czapek's solution agar growing somewhat restrictedly, attaining a diameter of 3.5 to 4.0 cm. in 10 to 12 days at 24°C., with surface more or less floccose, consisting of a loose network of interlacing vegetative hyphae arising from a compact basal felt, radiately furrowed with central colony area irregularly buckled (fig. 85A), lightly zonate, sporulating fairly abundantly, essentially uniform throughout the colony, with growing margin 2 to 4 mm. wide, white shading to court gray, then gnaphalium green (Ridgway, Pl. XLVII) with the development of conidial structures and becoming mineral gray in age; exudate limited, pale amber; odor lacking or indefinite; reverse at first in golden yellow shades becoming deep orange-brown near chestnut brown (R., Pl. XIV) in 2 weeks; penicilli abundantly produced, variable in size and complexity, strongly divaricate (fig. 84), borne either upon conidiophores arising from the substratum and varying in length up to 400 to 500μ by about 3.0 to 3.5μ

wide, or upon short branches from aerial hyphae, with walls conspicuously roughened, consisting of variously arranged, divergent structures, 1, 2, 3-verticillate (fig. 84B), with ultimate branchlets (metulae) usually about 10 to 20μ by 2.5 to 3.0μ, bearing sterigmata in clusters of 4 to 10 and measuring 7 to 9μ by 2.0 to 2.5μ, with definite conidium-bearing tips narrow but

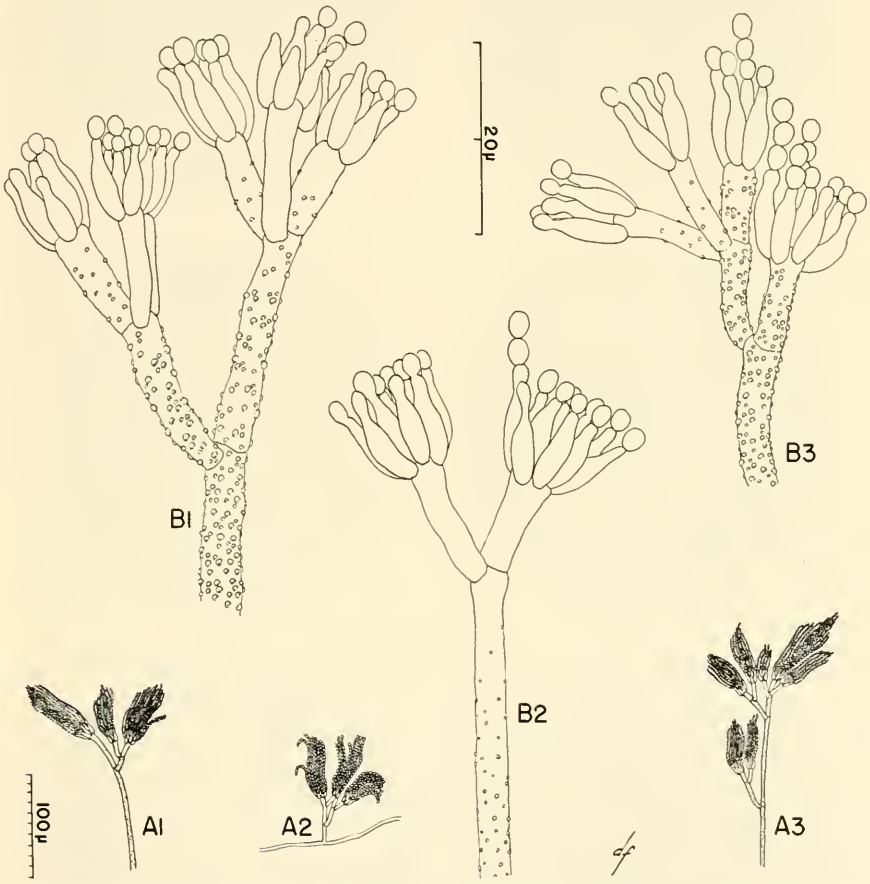


FIG. 84. *Penicillium canescens* Sopp. A_1–A_3, Habit sketches of representative penicilli showing tendency of conidial chains to form columns. B_1–B_3, Penicilli showing diversity of pattern and details of cellular structures.

comparatively short (fig. 84B); conidial chains arising from separate metulae tending to adhere into loose columns in young cultures, but becoming more or less divergent in age; conidia at first ovate to subglobose becoming globose at maturity with walls roughened mostly 2.0 to 2.5μ in diameter, occasionally larger.

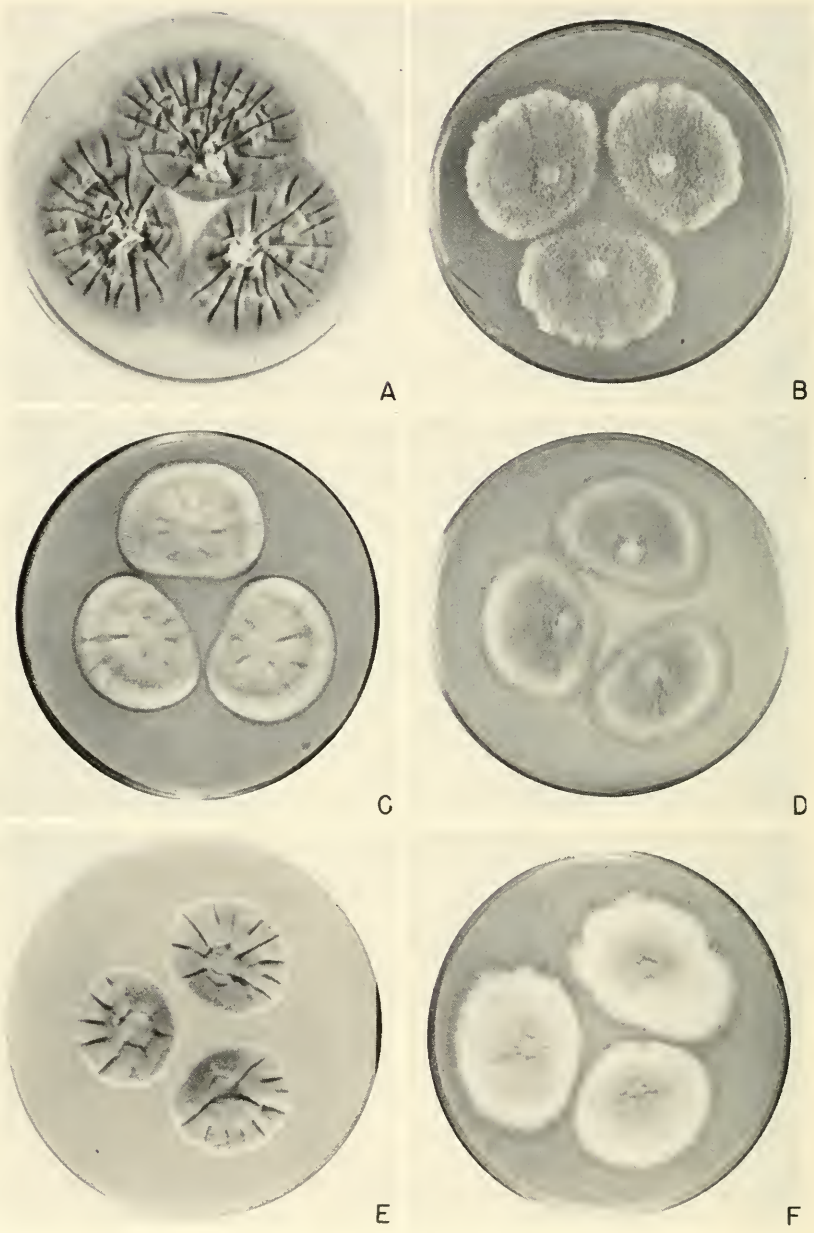


FIG. 85. *A* and *B*, *Penicillium canescens* Sopp, NRRL 910, on Czapek and malt agars at two weeks. *C* and *D*, *P. naligiovensis* Laxa, NRRL 911, as above. *E* and *F*, *P. jenseni* Zaleski, NRRL 909, also as above.

Colonies on steep agar growing more rapidly than on Czapek, sporulating somewhat more abundantly and more quickly developing gray shades, but otherwise essentially as described above; penicilli generally larger and more frequently borne upon long conidiophores arising from the substratum, but in general pattern duplicating the above.

Colonies on malt extract agar 2.5 to 3.0 cm. in 10 to 12 days, loose-textured, floccose, somewhat funiculose (fig. 85B), about 1 mm. deep, approximately gnaphalium green in color, evenly sporulating throughout; no exudate produced; reverse in rich brown shades; penicilli as on steep agar but showing a more definite tendency to produce persistent columns of spores.

Species description based upon culture NRRL 910 (Thom No. 2654) received from Miss Dale in England in 1912 and cited by Thom in 1930 as representing this species. A second strain of this culture which duplicates the preceding in all particulars, was obtained from the Centraalbureau in 1946 and has been included in the present study. The species is occasionally encountered in soil population studies.

Penicillium canescens is believed to be somewhat transitional between *P. janthinellum* and *P. nigricans*. Colonies grow more restrictedly than the members of the former series; they produce rich brown rather than purple-red colors in reverse, suggestive of *P. nigricans;* and conidia are globose and rough, although not so conspicuously so as in typical *P. nigricans* strains. While the character is less marked, conidial areas tend toward grays rather than blue-greens, further suggesting relationship to *P. nigricans*.

Penicillium nalgiovensis Laxa, in Zentbl. f. Bakt. etc. (II) **86:** 160–165. 1932.

Colonies upon Czapek's solution agar restricted, attaining a diameter of 3.0 to 3.5 cm. in 12 to 14 days at room temperature (24°C.), deeply floccose or lanose, consisting of a fairly close network of vegetative mycelia 2 to 3 mm. deep, lightly furrowed in a radial pattern (fig. 85C), somewhat zonate, at first white but after one week gradually developing conidial structures sparsely over most of the colony surface and becoming pale yellow-green, near celandine green (Ridgway, Pl. XLVII) in fruiting areas and usually assuming a flesh to pinkish tint in areas of purely vegetative growth, with marginal zone 3 to 4 mm. wide remaining uncolored, margins entire, not thinning perceptibly except in areas adjacent to other colonies; limited exudate produced as small droplets embedded in the colony, amber or vinaceous in color; odor lacking or indefinite; reverse in orange-red to maroon shades with surrounding agar similarly but less intensely colored;

conidial structures arising mostly as branches from aerial hyphae, less commonly directly from the substratum (fig. 86A), generally small and consisting of 2 or 3 or more clusters of sterimata borne irregularly and more or less terminally on conidiophores of variable dimensions up to 500μ

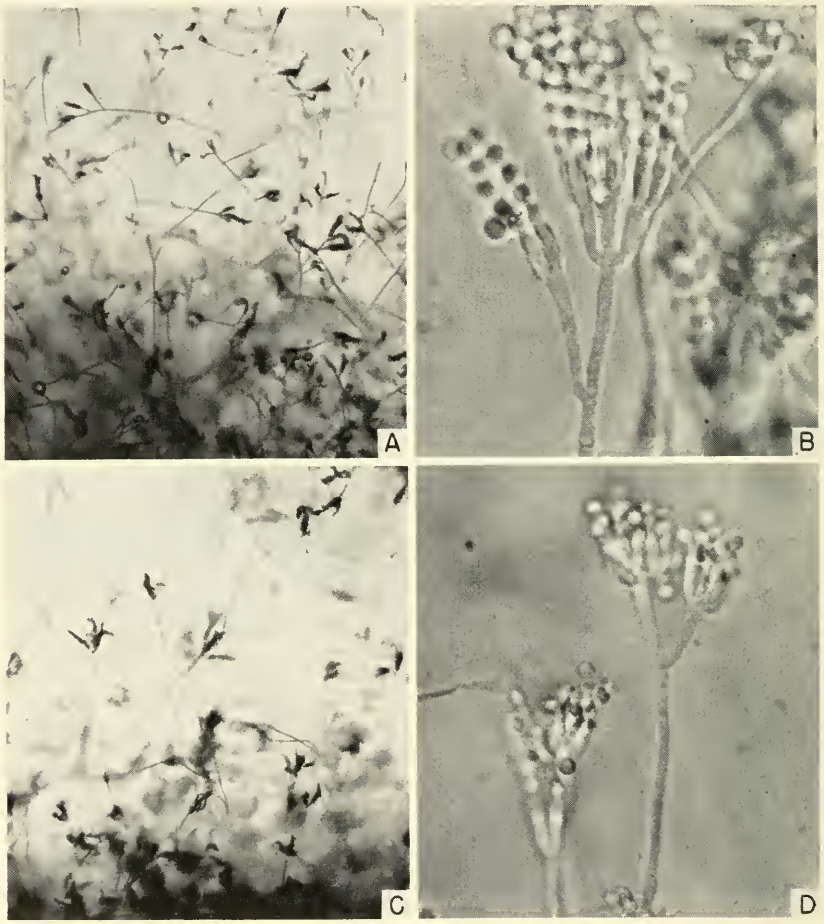


FIG. 86. *A*, *Penicillium nalgiovensis* Laxa, marginal colony area, × 85. *B*, Detail of a single penicillus in the same strain, × 1000. *C*, *P. jenseni* Zaleski, marginal colony area, × 85. *D*, Detail of penicilli in the same, × 1000.

or more by 2.5 to 3.0μ, with walls smooth or delicately roughened; penicilli strongly divaricate (fig. 86B), consisting variously of occasional branches, metulae and sterigmata, with branchlets (metulae) varying markedly in arrangement and in size but mostly 8 to 12μ by 2 to 3μ; sterigmata measuring 8 to 10μ by 2.0μ and lacking evident conidium-

bearing tubes are borne in small clusters of 3 to 6 and produce chains of spores which tend to adhere into narrow, short columns; conidia globose or nearly so mostly 3.2 to 3.6μ in diameter with walls thin, smooth or slightly irregular.

Colonies on steep agar growing somewhat more rapidly than on Czapek's solution agar, 3.5 to 4.0 cm. in diameter in 10 to 12 days, loose-textured, lanose, 2 to 3 mm. deep, more or less zonate with areas of vegetative growth definitely pink and areas of heaviest conidial development in fairly bright yellow-green shades (Ridgway, Pl. XLVII); exudate limited, as noted above; colony reverse deep maroon with surrounding agar similarly colored; penicilli as on Czapek agar.

Colonies on malt extract agar 3.0 to 3.5 cm. in 10 to 12 days, comparatively thin, loose-textured, lanose to velvety, plane, conspicuously zonate with marginal area 2 mm. wide, yellow-white and sterile (fig. 85D), shading to fairly bright yellow-green shades in areas of ripening conidia toward the colony center; no exudate; reverse in rich brown shades; penicilli as above but conidial chains longer and columns somewhat tangled and less well defined.

Species description based upon Laxa's type strain, NRRL 911 (Thom's No. 5337.2), received from him in April 1933. This culture was reported to be the principal species associated with the ripening of Ellischauer cheese (of the Camembert type), in Nalžovy, Southern Bohemia—hence the name. The production of appreciable red pigment is associated with the growth of this mold on cheese and in laboratory culture, and this character was emphasized by Laxa in his original description. On whey gelatine and whey agar, colonies were at first white, later shading to faintly greenish to greenish gray with colony reverse at first cherry, then blood red. Casein is digested rapidly with an accumulation of amino acids and ammonia.

Penicillium nalgiovensis is included in the Divaricata upon the basis of its fruiting structures, but the proper placement of this species remains in doubt. The general appearance of the colonies, the comparatively large globose conidia, the coloration of conidial areas, and finally the production of a diffusible red pigment in the culture medium all suggest relationship to *P. aurantio-virens* in the Lanata. There is little evidence, except for a deep flocculent colony, suggesting relationship to the *P. camemberti* series, although the mold was isolated from a similar type of cheese. It is entirely possible that we are here dealing with some member of the Lanata which during many years use in a particular cultural environment (cheese manufacture) has developed a rather unique cultural aspect and fruiting pattern. There is also the possibility that it is related to *P. psittacinum* Thom (see p. 445). In areas of heavy conidial production, and generally upon malt extract agar, colony colors approach the bright yellow-greens

which characterize that species. Lacking proof of either of these possibilities, however, we believe it desirable to base assignment upon morphological characteristics and place the species in the Divaricata.

Penicillium jenseni Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 494–495, Taf. 57. 1927. Thom, The Penicillia, pp. 346–347. 1930.

Colonies upon Czapek's solution agar growing restrictedly, attaining a diameter of 2.5 to 3.0 cm. in 12 to 14 days at room temperature (24°C.), consisting of a basal felt 500μ deep, strongly folded and wrinkled (fig. 85E), with central area raised or depressed, and with subcentral area strongly folded and radially furrowed, the agar underlying this portion of the colony commonly being pulled away from the culture dish, with surface appearing rather loose, finely granular, almost lanose, more or less zonate with margins 1 to 2 mm. wide, yellow-white, shading quickly through court gray to gnaphalium green (Ridgway, Pl. XLVII) with the ripening of conidia, sporulating abundantly throughout the colony; exudate not produced; odor lacking or indefinite; reverse uncolored to dull peach shades, fruiting abundantly on under surfaces that have pulled away from the culture plate. Penicilli conspicuously divaricate (fig. 86C), often appearing ramigenous, in larger structures usually consisting of a fairly definite terminal cluster of 2, 3, or more metulae, in smaller structures commonly not so arranged; conidiophores variable, smooth, arising from the substratum and ranging up to 500μ or more in length by 2.0 to 2.5μ wide, or borne as lateral branches upon trailing hyphae, commonly less than 100μ; metulae variable, commonly 8 to 10μ by 2.0μ; sterigmata usually in clusters of 5 to 10, compactly arranged (fig. 86D), usually 7 to 8μ by 2.0μ with fairly well defined conidium-bearing tubes, producing chains of conidia tending to adhere into loose columns; conidia globose to subglobose 2.0 to 2.5μ, with walls delicately roughened.

Colonies on steep agar growing more rapidly, about 5 cm. in 12 to 14 days at room temperature, conspicuously and closely furrowed, more or less zonate, with colony texture and color essentially as on Czapek; penicilli as described above.

Colonies on malt agar restricted, about 2.5 cm. in diameter, loose-textured, more or less floccose (fig. 85F), penicilli more consistently monoverticillate and tending to be ramigenous, with column development more strongly accentuated than upon the above substrata.

Species description based primarily upon culture NRRL 909 (Thom No. 5010.10) received from the Centraalbureau in 1928 as Zaleski's type; duplicated by a second strain of this same culture received from Baarn in April 1946. Isolates representative of this species are occasionally obtained from soil.

Penicillium jenseni is included in the Divaricata since the majority of the penicilli show this basic pattern. Many structures, however, appear clearly monoverticillate with individual penicilli borne singly on short branches or, more commonly, in irregular terminal groups in the manner typical of the Ramigena series (see p. 239). While we regard the present placement as correct, the probable relationship of the species to the Monoverticillata, possibly as a transitional form, should not be disregarded.

Penicillium chrzaszczi Zaleski (Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 464–466; Taf. 48. 1927) is believed to be synonymous with *P. jenseni* Zaleski as described above. The type culture of *P. chrzaszczi* as maintained in this Laboratory since 1928 (NRRL 903), and as returned to us in March 1946 from the Centraalbureau, strikingly resembles *P. jenseni* in culture upon Czapek's solution agar with or without the addition of steep liquor. On malt agar, colonies are somewhat heavier sporing but show the same tendency to grow restrictedly. The penicilli are more consistently biverticillate and generally appear in fairly compact fruiting structures (resembling *P. soppi*) with the ramigenous habit noted for *P. jenseni* less commonly observed. Conidiophores of NRRL 903 are smooth-walled, variable in length up to 400 to 500μ by 2.0 to 2.5μ; with metulae mostly about 8 to 10μ by 2.0μ, slightly enlarged at the apex, bearing sterigmata in compact clusters of 5 to 12 measuring about 6 to 8μ by 2.0μ; conidia globose to subglobose, 2.0 to 2.5μ in diameter with walls finely roughened. Sterigmata and metulae commonly appear more or less inflated but this character is not sufficiently constant to be of diagnostic value.

Occurrence and Significance

Members of the series appear to be widely but not abundantly distributed in nature. *Penicillium canescens* and *P. jenseni* are occasionally isolated from soil, whereas *P. nalgiovensis* is known only as the type isolated from cheese by Laxa in Bohemia.

Little information regarding biochemical or physiological characteristics is available. Bowen (1941) reported *Penicillium canescens* capable of destroying untreated flannel air filtration bags in less than a month in mines in South Africa. The best protection of the material was afforded by cuprinol, whereas various substances such as copper oleate, creosote and others gave good results for special purposes. Chrzaszcz and Tiukow (1929) reported limited production of citric acid by *P. jenseni* and *P. chrzaszczi*, two species that are now regarded as synonymous. Laxa (1932) briefly discusses the significance of *P. nalgiovensis* in the ripening of Ellischauer cheese.

Penicillium nigricans Series

Outstanding Characters

Colonies growing rather restrictedly upon most substrata, consisting of a close-textured basal felt with surface variously consisting of a network of trailing hyphae or appearing velvety; conidial areas in dull, often

dark, gray or olive-brown shades—almost black on some substrata; reverse typically developing deep orange-red shades; with exudate in many forms similarly colored.

Conidiophores varying greatly in length and in origin, arising either as short branches from aerial hyphae, as ascending hyphae or as separate conidiophores directly from the substratum.

Penicilli typically strongly divaricate, consisting of divergent metulae arising at one or more levels and bearing clusters of sterigmata giving rise to loose columns or tangled masses of conidia; monoverticillate penicilli not uncommon.

Conidia globose to subglobose, strongly echinulate in some forms, with color apparently concentrated in bars or tubercles between the outer and inner spore walls, smooth or nearly so in others.

Series Key

b. Ripe conidia typically in dull gray shades (scarcely showing any green) such as steel gray to dark olive gray (Ridgway), globose; colony reverse usually in yellow to deep orange shades..... *P. nigricans* series

1′. Conidiophore walls smooth or nearly so on all substrata.

aa. Conidia strongly echinulate with conspicuous color bars.

1″. Colonies heavily sporing, dull to dark gray in color. *P. nigricans* (Bainier) Thom

2″. Colonies floccose, light sporing, white or nearly so.... *P. albidum* Sopp

bb. Conidia delicately echinulate..... *P. kapuscinskii* Zaleski

2′. Conidiophore walls coarsely roughened, at least on malt agar.

aa. Conidia conspicuously echinulate..... *P. melinii* Thom

bb. Conidia smooth or nearly so..... *P. raciborskii* Zaleski

Members of this series are regular components of the mycoflora of soil and have been isolated from samples world-wide in origin. They seem to be especially abundant in forest soils upon organic constituents in the later stages of decomposition. They are occasionally isolated from other substrata subject to air and dust borne contamination. In his Monograph, Thom (1930) discussed these forms under the "*Penicillium nigricans-janczewskii* Series". Subsequent study has seemed to establish the identity of these two species, hence, their present consideration under the single name, *P. nigricans* series.

The series includes five species, as follows: *Penicillium nigricans* (Bainier) Thom, *P. kapuscinskii* Zaleski, *P. albidum* Sopp, *P. melinii* Thom, and *P. raciborskii* Zaleski. Of these species, *P. nigricans* is by far the most abundant, and if we expand our concept of this species to accommodate recurring variant types which show consistent but limited differences, the species and the series become almost one and the same thing. While realizing that they may represent little more than striking cultural variants from *P. nigricans,* we believe the user of the Manual will be benefited by

recognition of the following species: (1) *P. albidum*, to include forms with conidial structures and conidia essentially as in *P. nigricans*, but with colonies persistently white or nearly so; (2) *P. kapuscinskii*, to include forms with the general characters of *P. nigricans*, but with conidial areas less darkly colored, reverse in pale orange shades, and conidia less conspicuously roughened; (3) *P. melinii*, to include forms with conidiophores conspicuously roughened and penicilli commonly monoverticillate, but developing typical divaricate structures in sufficient numbers to necessitate placing the species here; (4) *P. raciborskii*, to include forms showing the general characteristics of the group but producing smooth conidia upon conidial structures with all walls conspicuously roughened.

Penicillium nigricans (Bainier) Thom, in The Penicillia, pp. 351–353, fig. 56. 1930.

Synonym: *Penicillium echinatum* Dale, in Biourge's Monogr., La Cellule **33:** fasc. 1, p. 278, Col. Pl. XI, and Pl. XVIII, fig. 104. 1923. Discussed without name as C_3 by Dale in Ann. Mycol. **12:** 42, Pl. III, figs. 51 and 52. 1914; and named by her in Ann. Mycol. **24:** 137. 1926.

Colonies upon Czapek's solution agar (Col. Pl. V) growing rather restrictedly, 2.5 to 3.0 cm. in 10 to 12 days at room temperature, forming a close-textured, fairly deep felt of delicate trailing hyphae and occasionally, but not regularly, bundles or ropes of hyphae, plane or increasingly wrinkled at higher temperatures toward 30°C., azonate at first, then more or less zonate at margin (fig. 88A); conidial areas in various shades of gray, steel gray, dark olive-gray, and Hathi gray (Ridgway, Pls. LI and LII), in age becoming mouse gray with little or no trace of green; reverse yellow to deep orange to deep ferruginous shades at various ages and under varying conditions; odor strong, suggesting certain species of *Actinomyces;* drops abundant, colorless or slightly yellowish; conidia-bearing hyphae variously short branches of aerial hyphae, or whole trailing hyphae showing thickened walls and bearing short branches with penicilli, or as separate conidiophores arising directly from submerged hyphae in marginal areas (figs. 87A and 88C); penicilli terminal on trailing hyphae or on short branches about 50μ long, consisting of variously diverging branchlets bearing few to many sterigmata and chains of conidia occasionally parallel but usually divergent or tangled in age, with individual chains commonly up to 50 to 75μ in length; conidiophores variable in length as indicated above, often very short, rarely more than 200μ in length by 2.5 to 3.0μ, with walls smooth but appearing internally granular; metulae strongly divergent, variable, about 8 to 12μ by 2.0 to 2.5μ with apices commonly inflated, each typically supporting a compact verticil of sterigmata simu-

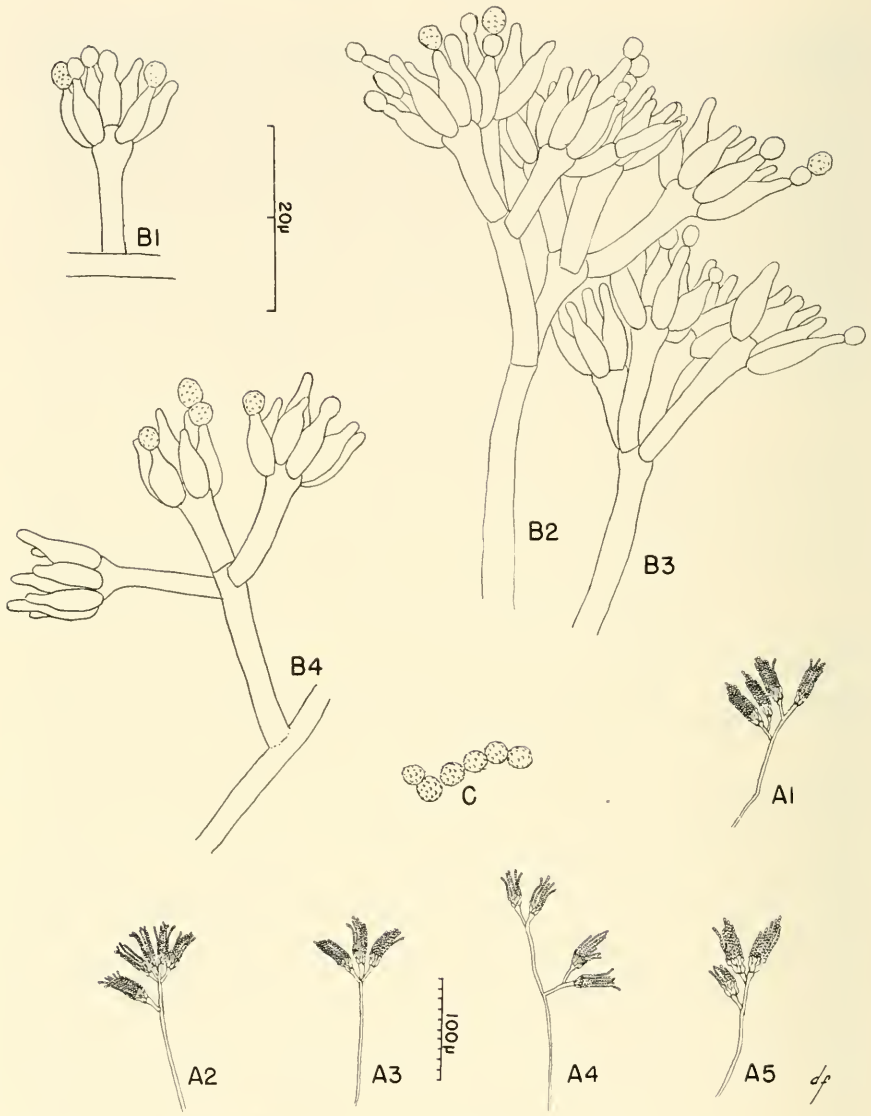


FIG. 87. *Penicillium nigricans* (Bainier) Thom. A_1–A_5, Habit sketches of representative penicilli illustrating strongly divaricate pattern. B_1–B_4, Penicilli as seen under oil immersion. *C*, Mature conidia, conspicuously echinulate.

lating a monoverticillate head (figs. 87B and 88D); sterigmata usually borne in clusters of 6 to 12, more or less divergent, about 7 to 8μ by 2.0μ; conidia 3.0 to 3.5μ in diameter, globose, echinulate or spiny (fig. 87C), appearing olive brown under high power.

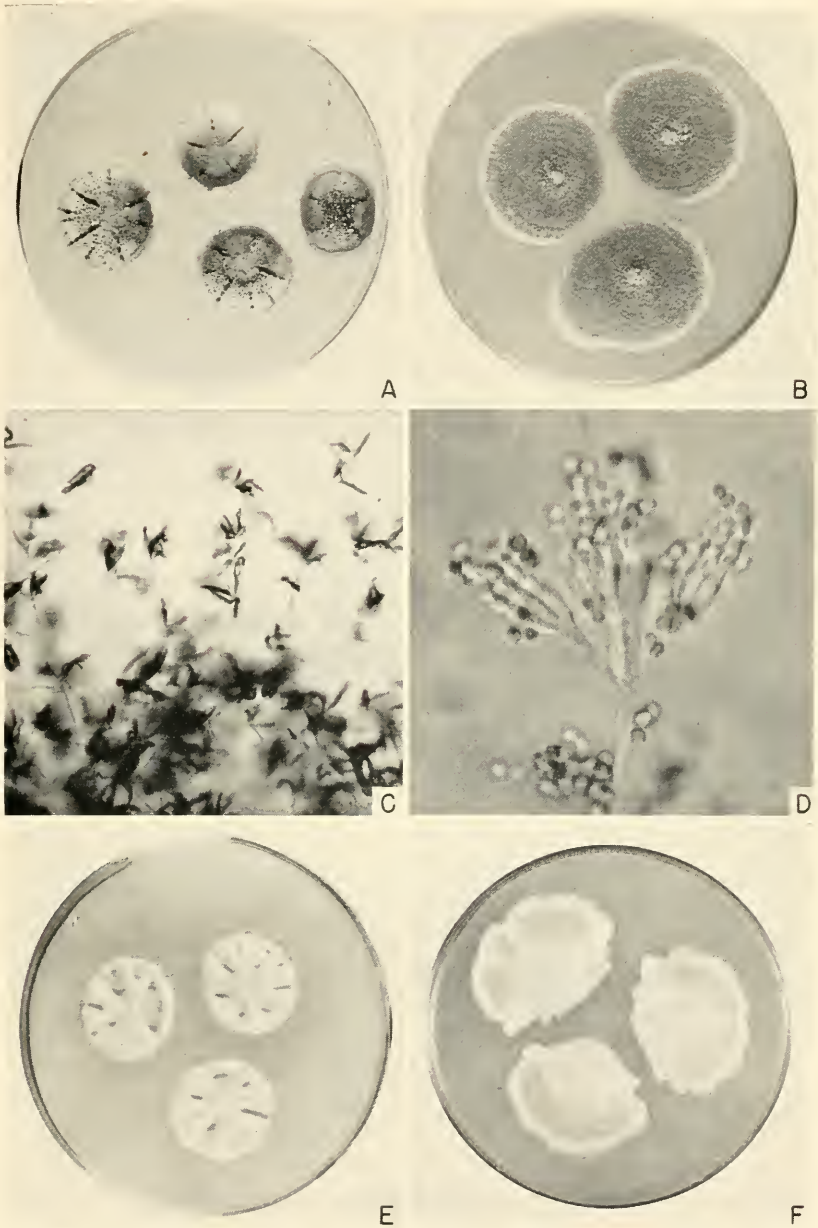


FIG. 88. *Penicillium nigricans* series. *A* and *B*, Colonies of *P. nigricans* (Bain.) Thom, NRRL 915, on Czapek and malt agars at two weeks. *C*, Marginal colony area of same strain showing divaricate penicilli, × 70. *D*, Detail of single penicillus, × 1000. *E* and *F*, *P. albidum* Sopp, NRRL 2043, on Czapek and malt agars at two weeks.

Colonies on steep agar essentially as above but more heavily sporing, darker in color near castor gray (R., Pl. LII), marked by fairly prominent but very narrow concentric zones, and producing less abundant exudate; penicilli as above but generally somewhat larger and more regularly branched.

Colonies on malt extract agar somewhat lighter in color, of looser-texture, heavy sporing (fig. 88B), with conidiophores long, up to 400 or even 500μ, arising primarily from the substratum and bearing comparatively large and strongly divaricate penicilli, consisting of few to several diverging, fairly definite columns of conidia up to 100μ in length.

The characterization given is drawn primarily from cultures NRRL 915 and 917. NRRL 915 was received by Thom in 1922 from the Bainier collection in Paris bearing the label "*Penicillium nigricans*" (nomen nudum). NRRL 917 was subsequently received from Prof. Westerdijk at Baarn as *P. echinatum* Dale. The two cultures are in fact identical, and for reasons explained by Thom in his Monograph (1930), the latter should be regarded as a synonym of *P. nigricans* (Bainier) Thom. Strains duplicating these are not infrequently isolated from soil.

The use of the name *Penicillum echinatum* by Rivolta in 1873, invalidates Miss Dale's use of it in 1926 for this organism. The name *P. echinulatum* Dale appears in Biourge's "Liste Onomastique" but not in Dale's papers. It is not explained.

Gilman and Abbott (1927, p. 293) assigned the name *Penicillium echinatum* Dale to Thom's description of the green members of the sub-section Divaricata in the series published by Pratt (1918) as the "Soil Penicillia". That description was purposely made broad enough to cover a series of forms now placed in *P. janthinellum* but which he did not wish to attempt to describe at that time. It did not, however, include the forms with globose, rough, conidia now under consideration.

Forms presenting essentially the cultural and morphological picture described above occur abundantly in soil and upon organic materials undergoing slow decomposition. Such forms may vary in specific details. In some cases they fail to show the characteristic golden orange coloration of colonies in reverse; in other cases sporulation is reduced and the strains appear more nearly floccose than the species description would indicate; while in still other cases the conidia, while roughened, are not conspicuously echinulate as in completely typical representatives of the species. All of these forms, however, produce conidia of some dark gray color; all produce conspicuously divaricate penicilli; and no satisfactory lines of separation warranting species recognition seem to exist between them. Zaleski (1927) examining Penicillia isolated from the forest soils of Poland, encountered some of these forms, regarded them as distinct, and described

3 new species. We have examined carefully the original description, and cultural observations made by Thom on Zaleski's strains prior to the publication of his Monograph in 1930. We have likewise re-examined the type strains in connection with the present study and we are led to believe that two of his three species represent merely normal strain divergence in the abundant and variable species, *Penicillium nigricans* (Bainier) Thom.

Penicillium swiecickii Zaleski (Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B pp. 474–476; Taf. 51. 1927) was described by Zaleski as having smooth-walled conidia about 2.3 to 2.8μ in diameter. The strain received as type from the Centraalbureau in July 1928, as noted by Thom (1930) produced spinulose conidia 3.0 to 3.5μ in diameter. Re-examined in the present study, Thom's earlier observations are confirmed but the conidia are not so conspicuously roughened as in typical members of the series, nor is the deposition of coloring matter as heavy as in most forms. The culture is regarded as a variant form of *P. nigricans* and it is believed that *P. swiecickii* Zal. should be regarded as a synonym.

Penicillium janczewskii Zaleski (Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 488–490, Taf. 55. 1927). Zaleski's description of this species and Thom's observations on the type strain received through the Centraalbureau fail to provide adequate bases for separation from *P. nigricans*. This was implied by Thom in 1930, in his consideration of the *P. nigricans-janczewskii* series. Examination of the type strain in the present study clearly reveals its identity with *P. nigricans* (Bainier) Thom. The culture differs from typical strains of *P. nigricans* only in producing colonies of somewhat closer texture and little or no yellow coloration in reverse. The irregular and divaricate penicilli and the conspicuously echinulate conidia are indistinguishable from those of *P. nigricans* (Bainier) Thom, with which Zaleski's species should be regarded as synonymous.

Penicillium albidum Sopp, in Monogr. pp. 186–187, Taf. XXI, fig. 144; Taf. XXIII, fig. 33. 1912. Thom, The Penicillia, pp. 350–351. 1930.

Sopp's description and figures for this species would seem to closely ally it with *Penicillium nigricans*. The conidia are described as "thorny" or rough, and at first green in color but soon becoming olive-green to gray and finally brown; colonies show surface growth uneven, fibrous, and consisting of irregularly branching and trailing hyphae, reverse is in reddish yellow shades. Thom (1930) discussed a strain (now lost from the Collection) under this name and placed the species in his *P. nigricans-janczewskii* series. A strain recently received from the Centraalbureau as an isolation of this species by Janke shows colonies essentially white, floccose, and with surface more or less uneven; conidial structures are very small and fragmentary, and consist almost exclusively of sterigmata borne separately or as strongly divergent spore-bearing cells. The conidia are conspicuously roughened, globose, and measure about 3.0 to 3.5μ, rarely 4.0μ. Except for the absence of well-formed divaricate penicilli, which

Sopp illustrates so clearly, the strain would seem to fit his description satisfactorily.

The species is retained to include strains producing conidial structures, often small, but essentially like *Penicillium nigricans* (Bainier) Thom, and with colonies tending to be floccose, light sporing, and generally white or nearly so (figs. 88E and F).

Represented in the NRRL Collection by No. 2043, received from the Centraalbureau in March 1946, as Janke's isolation.

Penicillium kapuscinskii Zaleski, in Bul. Acad. Polonaise Sci.: Math et Nat. Ser. B, pp. 484–485; Taf. 55. 1927. Thom, The Penicillia, pp. 355-356. 1930.

The following species description is taken from Thom's Monograph:

"Type strain growing fairly well about 20°C., very slightly at 30°C., or above; colonies on Czapek's solution agar about 20°C., restrictedly growing 15 to 20 mm. in diameter in twelve to fourteen days, appearing velvety but with very thin felt at base, buckled and radiately wrinkled sometimes in quadrants, with conidial area gray-green, deep olive gray (Ridgway, Pl. LI) at first, becoming drab in age (brownish drab, Ridgway, Pl. XLV) with mycelial hyphae, and marginal 3 mm. white, showing stolon-like hyphae reaching beyond the submerged mycelium and re-entering the substratum; hyphae very delicate; reverse in pale orange shades; drops, small, colorless, well distributed over the conidial area; conidiophores; (variable in length, arising from the substratum or from aerial hyphae—K.B.R.); penicillus partly monoverticillate, mostly variously showing one-branch, a group of sterigmata around the main axis at the first septum; branches (or metulae?) 12 to 15μ long; sterigmata 8 to 10μ by 2.0 to 2.5μ with conidial chains divergent; conidia 2.5 to 3.0μ, with delicate roughenings or spinulosity seen only under oil immersion.

"Culture No. 5010.12 received from Baarn in July 1928, tallied well enough with Zaleski's description to be accepted as type."

During the period since the publication of Thom's Monograph, the type strain of *Penicillium kapuscinskii* has been lost from our Collection. A culture, presumably type, however, was received from the Centraalbureau in April 1946 and is now maintained as NRRL 2147. Careful examination of this culture suggests the validity of the strain but fails to satisfy the description of the mold as it was known to us in culture from 1928 to 1930. The strain now produces colonies that are thin, closely wrinkled and very light sporulating with many, if not an actual majority, of the penicilli appearing monoverticillate. Conidial areas are in dull gray shades and conidia are finely roughened as indicated in Thom's (1930) description.

The species is retained to include occasional members of the *Penicillium nigricans* series which produce conidia that are globose but only finely roughened, and which are often less deeply colored in surface and in reverse than typical representatives of *P. nigricans* itself.

Penicillium melinii Thom, in The Penicillia, p. 273, 1930.

Colonies on Czapek's solution agar growing rather slowly, attaining a diameter of 2 to 3 cm. in 12 to 14 days at room temperature, velvety, close-textured, consisting of a tough basal felt bearing abundant conidial structures in most strains, strongly wrinkled in radiate pattern with cen-

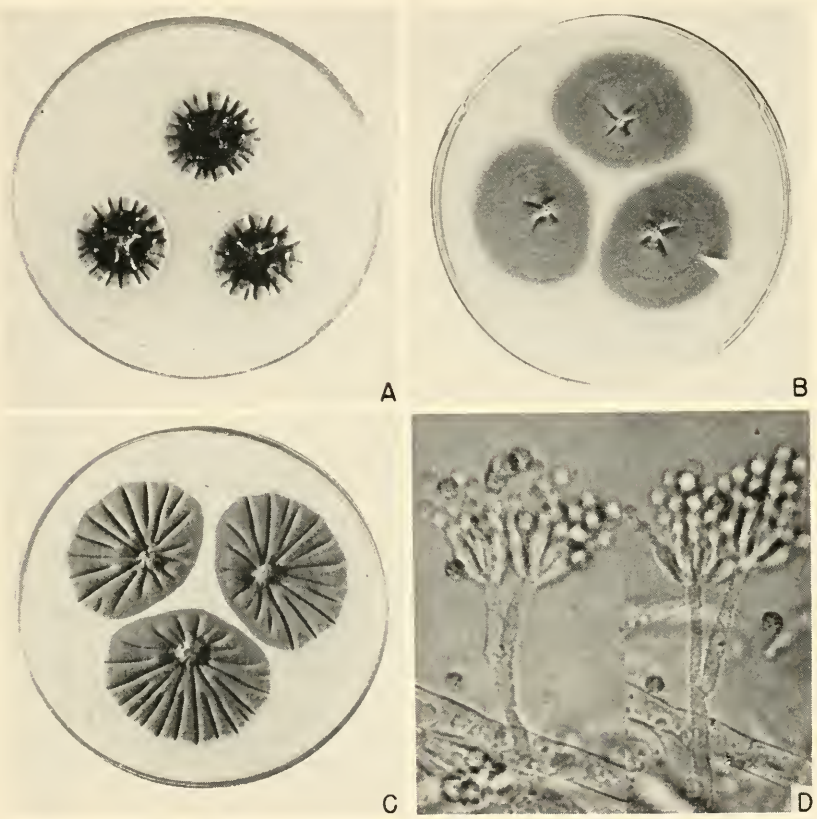


FIG. 89. *Penicillium melinii* Thom, NRRL 848. *A*, *B*, and *C*, Two-week-old colonies on Czapek, malt, and steep agars, respectively; note the very abundant (maroon) exudate on Czapek and its absence from other colonies. *D*, Detail of penicilli showing characteristic roughened conidiophores and rough, globose conidia, × 1000.

tral to subcentral areas generally raised (fig. 89A), growing margin narrow, white, shading quickly to yellow-green shades near gnaphalium to pea green (Ridgway, Pl. XLVII) becoming gray-green to deep grayish olive (R., Pl. XLVI) in age; odor moldy, not pronounced; exudate lacking in some strains to very abundant in others (fig. 89A), through orange-yellow to deep brown shades near russet (R., Pl. XV); reverse generally in the

same colors as the exudate and coloring the surrounding agar, in others at first grayish lavender, becoming purplish brown in age; penicilli variable, commonly monoverticillate but frequently consisting of a terminal group of diverging and unequal branches or metulae, irregularly arranged, developed either at the tip of the main axis or arising from lower nodes; conidiophores with walls granular-tuberculate (fig. 89D), usually less than 100μ long by 2.0 to 3.0μ; metulae usually 10 to 20μ by 2.0 to 2.5μ with walls granular; sterigmata in clusters of 5 to 10, compactly arranged, mostly 6 to 8μ by 2.0 to 2.5μ, broadest in central area with apices abruptly narrowed and tending to diverge, bearing conidia in chains up to 100μ in length, commonly divergent; conidia globose, about 3.0 to 3.5μ in diameter with walls conspicuously echinulate (fig. 89D).

Colonies on steep agar growing more rapidly, approximately 4.5 to 5.0 cm. in diameter in 12 to 14 days, velvety, strongly furrowed in a radial pattern, heavily sporing throughout (fig. 89C), with growing margin 0.5 to 1.0 mm. wide, white, quickly shading to deep grayish olive and to hair brown in age (R. Pl. XLVI); odor suggesting mushrooms; no exudate; reverse through dull lavender-gray shades to dull reddish brown; penicilli as described above.

Colonies on malt agar attaining a diameter of 3.0 to 4.0 cm. in two weeks, plane, velvety, heavily sporing (fig. 89B), quickly becoming deep grayish olive; conidial structures as described above but with stalks more coarsely roughened.

Species description centered upon NRRL 2041, received from the Centraalbureau in April 1946, as a strain contributed by Thom in 1930. This culture probably represents the type strain sent to Baarn at the time of the publication of Thom's Monograph. It differs from the original description, and from that presented above, only in the absence of exudate. NRRL 848, of unknown origin, on the other hand, produces colonies with exudate in strict agreement with the original description. The species is often encountered in soil dilution plates. The type strain was isolated by Dr. Elias Melin from forest soil.

Penicillium melinii is assigned to the Divaricata since an appreciable number of the conidial structures show the divaricate character typical of this group (fig. 89D). Many, if not an actual majority, of the penicilli, however, appear monoverticillate and a possible relationship to this group must be recognized. The globose, strongly echinulate conidia are strikingly similar to *P. nigricans*, as is also the general character of its branched penicilli. Color production likewise runs to orange-browns in both species. It differs from *P. nigricans* particularly in producing conidiophores that are conspicuously granulate whereas the conidiophores in *P. nigricans* are smooth-walled.

Penicillium raciborskii Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 454–455; Taf. 36. 1927. Thom, The Penicillia, pp. 318–319. 1930.

Colonies on Czapek's solution agar attaining a diameter of 3.0 to 4.0 cm. in 2 weeks, consisting of a fairly tough basal felt with surface somewhat flocculent, strongly wrinkled and buckled but lacking definite pattern, in white to light gray-green shades, conidial structures abundantly produced along inter-colony margins and less abundantly throughout, near tea green (Ridgway, Pl. XLVII); exudate limited, clear, colorless; odor slightly moldy, not pronounced; reverse dull peach, slowly developing vinaceous shades; penicilli biverticillate and asymmetrical, usually strongly divaricate, with conidial chains forming 2, 3, or more loose to fairly definite columns up to 75 or 100μ in length; conidiophores arising from the substratum or as branches from aerial hyphae, variable in length, rarely more than 200μ in length by 2.0 to 3.0μ in diameter, with walls generally appearing smooth; penicilli irregularly branched, with branches and metulae variable in size and often borne from the same level, the former commonly 10 to 18μ by 2.0 to 2.5μ, the latter 8 to 12μ by about 2.0μ with apices conspicuously enlarged to form dome-like vesicular areas up to 3.0 to 4.0μ or more in diameter; sterigmata crowded, closely parallel, in compact clusters of few to 10 or more, about 7.0 to 8.5μ by 1.5 to 2.0μ, with apices narrowed; conidia globose to subglobose, very small, thin-walled, about 1.5 to 2.0μ, with walls smooth or faintly granular.

Colonies on steep agar like the above but growing somewhat more rapidly and sporulating more heavily throughout the entire colony area, with growing margins white, quickly becoming dull gray-green near tea green (R., Pl. XLVII) and finally olive gray (R., Pl. LI) in age; exudate fairly abundant, slightly colored; odor more pronounced, moldy; reverse in dull reddish brown shades, penicilli as on Czapek.

Colonies on malt agar spreading broadly, 6 to 7 cm. in 10 to 12 days, comparatively thin, plane, with surface marked by a loose, overgrowth of flocculent hyphae, heavily sporing throughout in dull gray-green shades; exudate lacking; reverse in yellow-browns; penicilli as described above but often larger and with walls of conidiophores, branches, and metulae conspicuously roughened.

Species description centered upon NRRL 2150, received from the Centraalbureau in May 1946, presumably Zaleski's type; duplicated in essential particulars by Thom's notes on Zaleski's culture (now lost from our Collection) made in 1928 and reported in his Monograph (1930, pp. 318–319).

Penicillium raciborskii Zaleski was included in the Lanata by Thom in 1930. However, comparison with members of that section and with mem-

bers of the Divaricata leads us to believe that the true relationship of the species is with the latter. The species can best be assigned to the *P. nigricans* series, although it differs from the more representative members of this series by its more rapid growth and by producing conidia with walls smooth or nearly so.

In many species and strains, the character of conidiophore walls has been observed to vary upon different substrata. In no species have such differences surpassed those seen in *Penicillium raciborskii*, strain NRRL 2150. Upon Czapek's solution agar conidiophores are smooth or nearly so as reported by both Zaleski (1927) and Thom (1930). Upon malt agar, however, conidiophores, branches, and metulae are all conspicuously roughened. The importance of recording the substratum upon which observations are made is thus re-emphasized.

Occurrence and Significance

Members of the *Penicillium nigricans* series typically represent soil molds which are widely distributed in nature, but which seem to occur less frequently than other divaricate forms such as *P. janthinellum* and *P. lilacinum*. Comparatively little attention has been given to their possible role in decomposition processes. Gilman and Werkman (1936) reported *P. echinulatum* (= *P. nigricans*) to reduce the organic matter in steamed ground corn stalks by 16.9 percent within 21 days, as compared to 17.7 percent for *Trichoderma lignorum* and 30.0 percent for *Chaetomium funicolum*. Semeniuk and Ball (1937) found *P. melinii* to be one of several Penicillia commonly isolated from meat in cold storage lockers, but no special significance was attached to its presence.

Acid production by *Penicillium kapuscinskii*, *P. swiecickii* (see p. 329), and *P. janczewskii* was investigated by Chrzaszcz and Tiukow (1929). In a subsequent study the nitrogen metabolism of *P. janczewskii* in relation to citric acid formation was investigated Using cane sugar (8%) as a carbon source, acid production tended to increase when certain amino acids were added to the medium. *Penicillium jenseni* was reported to produce both citric and oxalic acids.

Brian, Curtis, and Hemming (1946) reported the production by *Penicillium janczewskii* of an antibiotic substance possessing fungistatic properties. The substance, termed "curling factor", was observed to cause unusual stunting and distortion of the germ tubes and hyphae of *Botrytis allii* and other fungi. The factor was produced in maximum amount in media containing 75 percent glucose, and could be removed by extraction with chloroform, ether, *n*-butyl alcohol, or adsorption on activated charcoal. Upon further purification, colorless crystals were obtained. Yields up to 150 mg./liter were reported. More detailed information regarding

the chemical and physical properties of the "curling factor" were reported by McGowan (1946).

More recently, Grove and McGowan (1947) have reported that the "curling factor" produced by *Penicillium janczewskii* is identical with griseofulvin, $C_{17}H_{17}O_6Cl$, which was isolated in 1939 by Oxford, Raistrick, and Simonart from *P. griseo-fulvum*. Curtis and Grove (1947) have reported the production of a red pigment possessing anti-bacterial and fungistatic properties by a member of this series, as yet not identified to species. Chemical and biological investigations of the pigment are in progress.

Chapter IX

ASYMMETRICA

Sub-section: VELUTINA

This section includes species of *Penicillium* with asymmetric penicilli that are characteristically developed in a dense and even stand to produce a velvety effect. Strictly speaking, it is typified by species in which the vegetative mycelium is largely or wholly submerged, and the aerial portion of the colony consists of conidiophores standing like a field of wheat—the conidiophores being comparable to the wheat culms and the conidial heads representing the heads of grain. Actually, many gradations are encountered, and in practice, the term velvety is broadened to include species that are obviously related but in which conidiophores arise from a basal network of interwoven aerial hyphae. The section does not include any forms in which colonies are definitely floccose or lanose; or in which aerial growth is collected into ropes or funicles; or in which conidiophores are aggregated into tufts or fascicles. Species developing these characteristics are considered in other sub-sections which follow, namely: Lanata, Funiculosa, and Fasciculata. Evidence of cross-relationship between these different sub-sections has been observed in a limited number of cases, but on the whole lines of separation are fairly definite and easily determinable.

Six series are recognized within the Velutina. These include some of the most abundant and the most important of all the Penicillia from an agricultural and industrial point of view. The series, which are centered around well known and easily recognized species, may be briefly differentiated as follows: *Penicillium citrinum* series, characterized by asymmetric penicilli that usually consist of terminal verticils of metulae, bearing sterigmata with conidial chains typically adherent in divergent columns. *Penicillium chrysogenum* series, characterized by penicilli that are often rebranched below the level of the metulae. Colonies are usually marked by bright to pale yellow pigmentation in exudate and reverse. Conidial chains commonly adhere into well-defined columns. Members of the series produce the antibiotic penicillin in varying amount. *Penicillium oxalicum* series, common in soil, is characterized by strongly elliptical conidia which in newly isolated strains often form heavy crusts. *Penicillium digitatum* series, represented by the single species of the same name, is responsible for the so-called "green rot" of citrus fruit. *Penicillium roqueforti* series, including the molds used for the production of Roquefort-type cheeses, is characterized in culture by colonies with arachnoid margins and by conidiophores with walls conspicuously roughened.

Penicillium brevi-compactum series, marked particularly by the development of unusually compact penicilli in which all cellular elements are closely compacted and appressed. Extension of the colony margin by stolon development is characteristic of most forms on certain substrata.

Page

Key to the Velutina

I. Penicilli seldom branched below the level of metulae, with metulae often more or less divergent ..... *P. citrinum* series 338
  A. Metulae typically in verticils of 2 or 3, often unequal in length, conidial chains not forming well-defined columns; conidia elliptical to subglobose ..... *P. corylophilum* Dierckx 341
  B. Metulae typically in verticils of 3 to 5, bearing crowded sterigmata and conidial chains usually in well-defined columns; conidia globose to subglobose.
    1. Colonies showing bright yellow to orange-pink shades in reverse; conidial areas in bright blue-green shades; usually producing citrinin. *P. citrinum* Thom 345
    2. Colonies showing dull yellow to olive buff shades in reverse; conidial areas in dull blue-green or yellow-green shades; not producing citrinin ..... *P. steckii* Zaleski 350
  C. Metulae typically in verticils of 5 to 8, closely compacted; conidial chains not in well-defined columns ..... *P. paxilli* Bainier (see *P. brevi-compactum* series)

II. Penicilli typically rebranched below the level of metulae, with main axes and branches terminating in verticils of metulae.
  A. Penicilli commonly long, with elements loosely arranged and often divergent.
    1. Conidiophores smooth-walled; colony margin not appearing arachnoid (cobwebby).
      a. Colonies typically producing abundant yellow pigment in exudate and colony reverse; conidial chains often adherent into well-defined columns; conidia less than 5μ in long axis; subglobose to elliptical ..... *P. chrysogenum* series 355
        1′. Conidia elliptical, or occasionally subglobose.
          aa. Colonies usually showing abundant yellow exudate and yellow pigmentation in reverse ..... *P. chrysogenum* Thom 359
          bb. Colonies showing pale or colorless exudate, and vinaceous to brownish fawn colors in reverse ..... *P. meleagrinum* Biourge 364
        2′. Conidia globose to subglobose.
          aa. Colonies velvety, heavily sporing, in rich blue-green shades, often comparatively thin ..... *P. notatum* Westling 367
          bb. Colonies loose-textured, floccelent, often lightly sporing, comparatively deep ..... *P. cyaneo-fulvum* Biourge 371
      b. Colonies not producing yellow pigment in exudate or colony reverse; conidia commonly 5.0μ or more in long axis, strongly elliptical.
        1′. Conidia elliptical, fairly uniform in size; common in soil. *P. oxalicum* series 376

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aa. Colonies plane or nearly so, conidia often forming deep crusts, conidial chains appearing "silky" when viewed under low power.....*P. oxalicum* Currie and Thom 378
bb. Colonies radially furrowed, not forming deep crusts, reverse in maroon shades.....*P. atramentosum* Thom 381
2′. Conidia strongly elliptical to cylindrical, varying greatly in size and often very large; penicilli very irregular, often fragmentary; produces "green" citrus rot.....*P. digitatum* series 385
P. digitatum Sacc. 386
aa. Conidia white; otherwise duplicating the species.
P. digitatum Sacc. var. *californicum* Thom 390
2. Conidiophores typically rough-walled; colony margins usually appearing arachnoid.....*P. roqueforti* series 392
a. Colonies broadly spreading, with surface plane or nearly so; margins thin, appearing arachnoid..... *P. roqueforti* Thom 395
b. Colonies restricted, strongly wrinkled or furrowed, margins hardly arachnoid.....*P. casei* Staub 401
B. Penicilli comparatively short, compact, with all elements closely appressed.....*P. brevi-compactum* series 404
1. Penicillus typically showing one or more side branches below the level of metulae.
a. Conidiophores coarse, with branches and metulae commonly inflated.....*P. brevi-compactum* Dierckx 407
b. Conidiophores thinner, flexuous, with branches and metulae not inflated.....*P. stoloniferum* Thom 412
2. Penicillus typically consisting of a single, crowded, terminal verticil of 5 to 8 metulae.....*P. paxilli* Bainier 414

Penicillium citrinum Series

Outstanding Characters

Colonies growing rather restrictedly on Czapek's agar, typically thin but varying in depth and general texture depending upon the species and strain, fruiting surface appearing velvety, usually medium to heavy sporing, in bluish green to yellowish green shades, often producing abundant exudate ranging from colorless to bright yellow; reverse usually in yellow, dull orange or light brownish shades, in one species becoming almost black.

Conidiophores erect, comparatively short, mostly less than 200μ in length, arising as a dense stand from the substratum or the basal felt, less commonly from aerial hyphae in more floccose strains, smooth-walled, usually unbranched except in the terminal area.

Penicilli typically consisting of a terminal cluster of 3, 4, 5, or occasionally more metulae, each bearing a crowded cluster of parallel sterigmata and chains of conidia commonly (but not consistently) adherent in well-defined and rather divergent columns. The penicillus commonly

presents the aspect of a cluster of monoverticillate fruits when viewed under low magnifications.

Conidia comparatively small, mostly 2.5 to 3.2μ, globose to elliptical depending upon the species and strain, with walls smooth or delicately roughened.

Production of the antibiotic citrinin is characteristic of the principal species.

Series Key
(See General Key to Velutina)

Members of the series are very abundant and widely distributed in nature. They are encountered among the isolates from almost all soils examined, and have occurred with greater frequency than any other series of Penicillia among the isolates from deteriorating military equipment submitted to us for identification. They appear to be particularly abundant in tropical and sub-tropical areas.

Colonies of different species and strains vary appreciably in texture, color, and the abundance of fruiting structures when grown upon Czapek's solution agar. They are generally rather restricted, more or less radially wrinkled, and are characterized by the presence of varying amounts of exudate ranging from colorless to bright yellow. Upon malt extract agar, colonies vary greatly depending upon the species, with this character providing a useful and generally reliable key to species identity: in *Penicillium citrinum* Thom, colonies are consistently restricted and are generally smaller than on Czapek, plane, heavy sporing, commonly up to 300μ or more deep, and with reverse typically in orange-yellow shades. In *P. corylophilum* Dierckx, on the other hand, colonies are broadly spreading, thinner, with reverse in light brown to dark shades approaching black in localized areas or sectors. In *P. steckii* Zaleski, colonies tend to be intermediate between the above both in rate of growth and in general colony texture.

The outstanding diagnostic feature of the series lies in the distinctive character of the penicilli. Typically, these consist of terminal clusters of metulae arising from unbranched conidiophores. The metulae tend to diverge. Sterigmata vary in number but generally range from 5 to 10 per metula, are comparatively short, and bear conidia from apices which are not conspicuously pointed. The sterigmata are generally crowded and essentially parallel and in most forms tend to bear conidial chains in compact columns which superficially suggest separate, monoverticillate penicilli.

Three species are recognized, namely: *Penicillium citrinum* Thom, *P. steckii* Zaleski, and *P. corylophilum* Dierckx.

Penicillium citrinum is by far the most abundant and the most variable,

the range of which is indicated in the discussion of the species and indicated in some degree in fig. 92. Some citrinin is almost invariably produced by strains assignable to this species upon cultural and morphological grounds, thus providing additional evidence of close relationship. The characteristics of the species are, in general, those of the series as listed above.

Penicillium steckii differs in showing less pigment both in colony reverse and in its exudate, in developing dull yellow-green rather than blue-green shades in conidial areas, in growing somewhat more rapidly upon most substrata, and in its failure to produce citrinin.

Penicillium corylophilum produces thinner and usually closer-textured colonies, with penicilli often smaller, less regular in pattern and showing less well-defined columns of conidia. The species does not produce citrinin.

The *Penicillium citrinum* series seems to be comprised of a group of transitional species. *Penicillium citrinum* Thom appears to be intermediate between monoverticillate forms with ramigenous penicilli on the one hand and members of the *P. chrysogenum* series on the other. Occasional cultures are seen, such as that upon which Thom (1930) based his species *P. sartoryi* (see p. 349), which shows the loose irregular branching habit of certain monoverticillate species coupled with the general appearance and coloration of typical *P. citrinum*. It is believed significant that such cultures produce citrinin. On the other hand, occasional cultures are encountered which culturally and structurally suggest *P. notatum* Westling, and such strains by spectrum plate tests appear to produce both citrinin and penicillin.

Penicillium corylophilum Dierckx, as known to us by the type and other representative strains, appears to be intermediate between such forms as *P. citrinum* and members of the ramigenous series of the Monoverticillata. Maximal conidial structures show the characteristic biverticillate pattern of the present series, hence this placement. Oftentimes, however, an equal number of penicilli appear monoverticillate, with such structures variously and irregularly arranged.

Penicillium steckii Zaleski, in the sense of this Manual, appears to be transitional toward the Divaricata, particularly in the direction of *P. jensenii* Zaleski. Both species show reduced pigmentation, both produce penicilli consisting of terminal verticils of metulae, whereas neither produces citrinin or any other known antibiotic. *Penicillium steckii* is likewise suggestive of the *P. raistrickii* series in the Divaricata, but differs from the latter in its failure to develop sclerotia and in producing smooth rather than rough-walled conidiophores. Finally, *P. steckii* is suggestive of *P. paxilli* Bainier in the *P. brevi-compactum* series, differing from that species primarily in the smaller number and less crowded arrangement of its metulae.

Penicillium corylophilum Dierckx, in Soc. Sci. Brux. **25:** 86. 1901. In Biourge, Monogr., La Cellule **33:** fasc. 1, pp. 266–267; Col. Pl. IX and Pl. XIV, fig. 83. 1923. Thom, The Penicillia, pp. 254–255. 1930.

Colonies upon Czapek's solution agar growing somewhat restrictedly, attaining a diameter of 2.5 to 3.0 cm. in 10 to 12 days at room temperature, consisting of a closely woven basal felt about 200 to 350μ deep, tough, tearing irregularly, becoming velvety in appearance with the development of abundant conidial structures (fig. 91A), strongly furrowed in a radial pattern, at first white to cream-colored, becoming blue-green with the development of conidia and shading through artemisia green (Ridgway, Pl. XLVII) or glaucous-gray (R., Pl. XLVIII) shades when young to olive brown (R., Pl. XL) in age, at times more or less zonate, producing limited exudate as small, colorless droplets; odor evident but not distinctive; reverse in dull light brown or fuscous shades; conidium production often beginning late (after 8 to 10 days), appearing first in the more crowded marginal areas of adjacent colonies but soon developing more or less uniformly over the whole colony surface; conidiophores arising mostly from the substratum in narrow marginal areas, but elsewhere as branches from interwoven hyphae which comprise the basal felt, mostly 50 to 100μ by 2.2 to 2.5μ, but ranging from 40 to 200μ in length, generally unbranched, smooth-walled throughout; penicilli variable in form and dimensions, typically biverticillate and asymmetric but with monoverticillate structures sometimes predominating; penicilli typically consisting of 2 to 3 metulae, variable in length (figs. 90A_2 and 91D), mostly 12 to 20μ by 2.0 by 3.0μ, each supporting a group of 4 to 8 sterigmata measuring about 8 to 12μ by 2.0 to 2.5μ, with individual cells occasionally longer in otherwise typical clusters; conidia subglobose to elliptical, mostly 2.5 to 3.0μ in long axis, with the more elliptical cells commonly measuring 3.0 to 3.2μ by 2.5 to 2.8μ, smooth-walled, in long, loosely adherent or tangled chains (fig. 90A_1).

Colonies upon steep agar somewhat restricted, attaining a diameter of 3.0 cm. in 10 to 14 days, strongly wrinkled in a predominantly radiate pattern, more or less angular in outline (fig. 91B), heavily and uniformly sporing, velvety, with conidiophores arising directly from the substratum or as branches from interlacing hyphae forming a loose network just above the agar surface, sage green (R., Pl. XLVII) in younger fruiting areas to deep olive gray (R., Pl. LI) at colony centers, droplets few and colorless, reverse uncolored to light brown; penicilli as on Czapek but tending to be slightly larger.

Colonies upon malt extract agar spreading broadly (fig. 91C), measuring 8 to 9 cm. in 10 to 14 days at room temperature, plane, strictly velvety, thin, heavy sporing, gnaphalium green through pea green to celandine

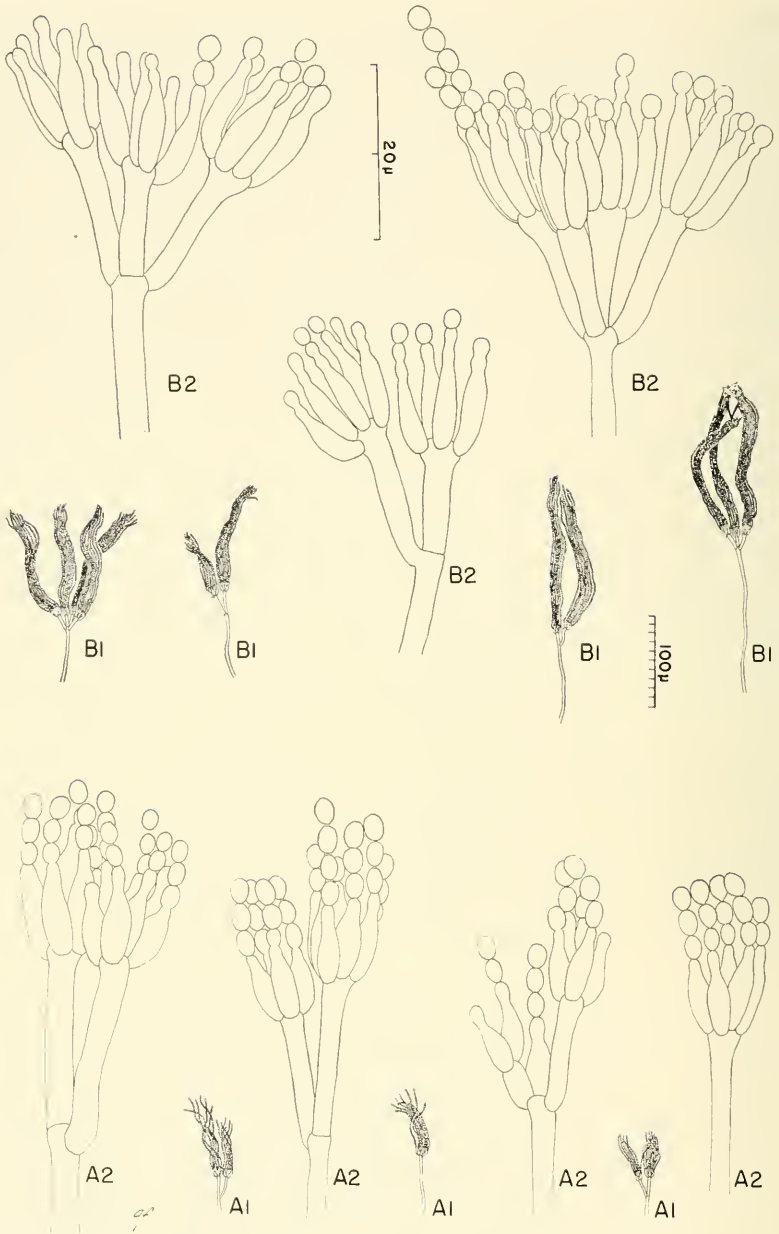


FIG. 90. *Penicillium citrinum* series. *A*, *P. corylophilum* Dierckx: A_1, Habit sketches of conidial structures; A_2, Detailed drawings of representative penicilli. *B*, *P. citrinum* Thom: B_1, Representative penicilli under low magnifications showing characteristic columns of conidia; B_2, Detailed drawings, greatly enlarged.

green (R., Pl. XLVII) no exudate produced; reverse in light brown to dark shades approaching black in localized sectors; penicilli as on steep agar.

Typically the metulae comprising a single penicillus tend to diverge, giving the impression of a group of two or three (very rarely more) monoverticillate structures. The metulae may or may not be of equal length,

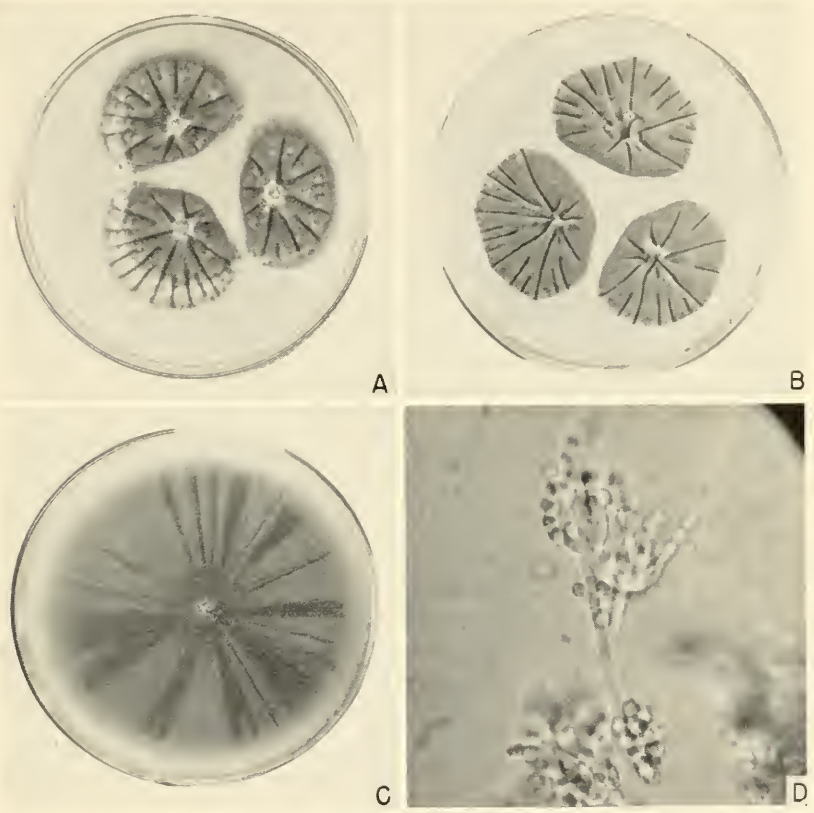


FIG. 91. *Penicillium corylophilum* Dierckx, NRRL 802. *A*, *B*, and *C*, Two-week-old colonies on Czapek, steep, and malt agars; note particularly the somewhat angular colony pattern on steep agar and the broadly spreading growth on malt agar. *D*, Detail of a single penicillus in another typical strain, NRRL 793; × 750.

further contributing to this general aspect. Individual spore chains sometimes adhere in loose columns, but these are poorly formed at best and are not produced with any degree of regularity comparable to *Penicillium citrinum* (fig. 90) and *P. steckii*. The spore chains arising from a single cluster of sterigmata usually show no definite arrangement and in

crowded fruiting areas commonly become interlaced with those of adjacent penicilli.

Species diagnosis is based primarily upon the following cultures: NRRL 802 (Thom's No. 4733.42), received in 1924, from Professor Biourge as his No. 78, which is presumably type; NRRL 803, received in 1927, from Dr. C. E. Burnside, apiculturist, as a common infection in brood combs; and two cultures received as *Penicillium corylophilum* Dierckx from the Centraalbureau in February, 1946. The species is also represented by NRRL 799, brought to our Laboratory in 1936 by Dr. Paul Simonart as Biourge's culture (type?) of *P. chloro-leucon* Biourge. It is further represented by NRRL 793 from Biourge, in 1924, as his type of *P. obscurum* Biourge, and a culture of like origin, bearing the same name, from the Centraalbureau in June, 1946.

Penicillium corylophilum is fairly abundant in nature and widely distributed. It is isolated occasionally from soil, and several strains have been encountered recently among the molds submitted to us for diagnosis by various groups of investigators studying the tropical deterioration of military equipment. Among the latter are included strains from stations in the South Pacific area, Panama, Florida, and elsewhere.

The species is placed in the *Penicillium citrinum* series solely upon cultural and morphological considerations. It differs from *P. citrinum* in a number of particulars, notably in an absence of any yellow pigmentation and in its inability to produce citrinin.

Careful examination of the descriptions and published figures of *Penicillium corylophilum* Dierckx, *P. obscurum* Biourge, *P. chloro-leucon* Biourge, and *P. sumatrense* v. Szilvinyi, fail to reveal any marked differences in either cultural behavior or structural detail. For this reason, and in the light of recent studies, it is our considered opinion that these species were separated upon inadequate criteria. The differences originally observed were probably not greater than those known to exist among the representatives of many other cosmopolitan species. The above description of *P. corylophilum* Dierckx is sufficiently broad to include the following:

Penicillium obscurum Biourge (Monogr., La Cellule **33**: fasc. 1, pp. 267–269; Col. Pl. VIII and Pl. XIV, fig. 80. 1923) culturally and morphologically closely approximates *P. corylophilum* Dierckx. Biourge himself suggested a close relationship between these species and Thom (1930, pp. 251 and 255) failed to observe adequate bases for separation. In the present study, a detailed comparison of cultural habits and microscopic structures in Biourge's type for *P. obscurum*, NRRL 793 (Thom's No. 4733.91, received in 1924 from Professor Biourge as his No. 120), and representative strains of *P. corylophilum* have been made, and we are forced to conclude that we are dealing merely with different strains of the same species. *Penicillium obscurum* Biourge, the most recently described, is therefore regarded as a synonym.

Penicillium chloro-leucon Biourge (Monogr., La Cellule **33:** fasc. 1, pp. 270–271; Col. Pl. VIII and Pl. XIV, fig. 79. 1923) is believed to be synonymous with *P. corylophilum* Dierckx. As described and figured by Biourge, this species produced penicilli more consistently biverticillate than *P. corylophilum* or *P. obscurum;* but like them, was characterized by colonies showing dark in reverse, monoverticillate penicilli in greater or less numbers, and subglobose to elliptical conidia measuring about 3.0 to 3.5μ in long axis. If NRRL 799, brought by Dr. Paul Simonart in 1936 from Professor Biourge's Laboratory, represents Biourge's type strain of *P. chloro-leucon,* and there are reasons to believe that it does, then this species should be considered synonomous with *P. corylophilum* Dierckx, since this strain duplicates NRRL 802 and NRRL 803.

Penicillium sumatrense v. Szilvinyi, in Archiv f. Hydrobiologie Suppl. Bd. XIV; Tropische Binnengewasser Bd. VI, pp. 551–552, 1936. Careful cultural examination of the type strain, NRRL 779, received from Professor Westerdijk in 1936, shows a striking similarity to *P. corylophilum* Dierckx. Microscopic examination likewise shows duplication in structural details, with the penicilli usually consisting of a terminal cluster of 2 or 3 or more metulae. A second substrain of v. Szilvinyi's type, received from the Centraalbureau in May 1946, completely duplicates NRRL 779. We are, therefore, led to believe that this species should be dropped, and the culture henceforth regarded as representing *P. corylophilum* in the broad sense that the species is considered in this Manual. NRRL 779 shows slightly more limited growth on malt and somewhat longer conidiophores than many strains of *P. corylophilum,* but neither difference is greater than that normally expected among different strains of a single species.

Penicillium citrinum Thom, in U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, pp. 61–63, fig. 22. 1910. Emended by Thom in The Penicillia, pp. 256–257, fig. 34. 1930.

Synonym: *P. aurifluum* Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 250–252, Col. Pl. VII and Pl. XI, fig. 64. 1923.

Colonies on Czapek's solution agar (Col. Pl. VI) growing restrictedly, generally 2.0 to 2.5 cm. in diameter in 10 to 14 days at room temperature (24 to 25°C.), typically furrowed in a radial pattern (fig. 92A), often conspicuously so, ranging from velvety in most strains, more or less floccose in some (fig. 92E), to close-textured and almost leathery in others, conidial production varying from light to abundant in different strains and to some degree depending upon the number of colonies in the culture plate, zonation more or less evident in some strains, not in others; conidial areas in blue-green shades near celandine green (Ridgway, Pl. XLVII) at first, becoming artemisia green to lily green (R., Pl. XLVII) at maturity and finally mouse gray to deep olive gray (R., Pl. LI) in age, conidium production often occurring late (after 8 to 10 days) and commonly not uniformly throughout the whole colony, generally heaviest in marginal to submarginal areas; abundant exudate in the form of pale yellow to straw colored droplets of varying size usually produced; pronounced mushroom odor in some strains, not marked in others; reverse usually in yellow to orange shades,

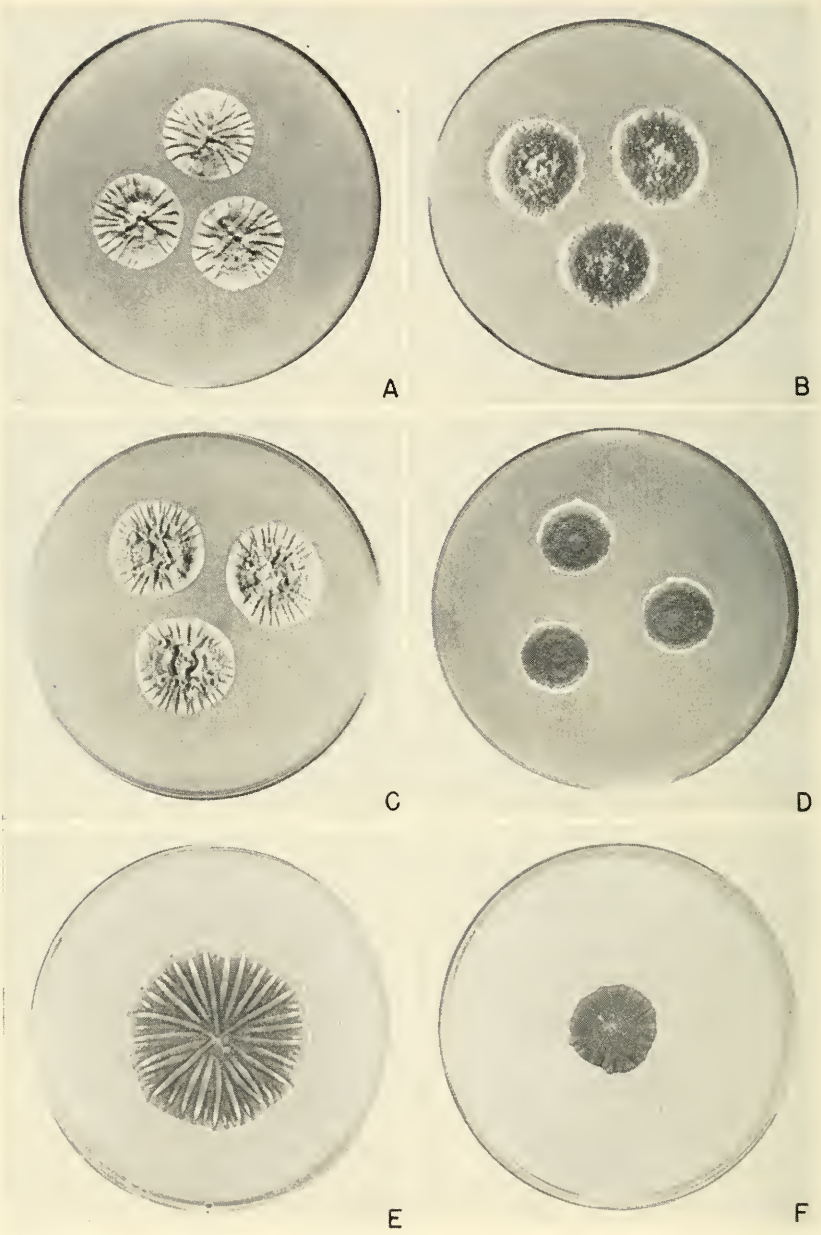


FIG. 92. *Penicillium citrinum* Thom. *A* and *B*, NRRL 806 on Czapek and malt agars at two weeks. *C* and *D*, NRRL 1842 on the same substrata, same age. *E* and *F*, NRRL 1841, on steep and malt agars.

PLATE VI

TOP: Penicillium citrinum Thom, NRRL 806, on Czapek's solution agar, 12 days. *CENTER: Penicillium roqueforti* Thom, NRRL 849, on Czapek's solution agar, 10 days. *BOTTOM: Penicillium stoloniferum* Thom, NRRL 859, on Czapek's solution agar, 12 days. (Color photographs by Haines, Northern Regional Research Laboratory. Reproduced through co-operation of Chas. Pfizer & Co., Inc.)

the agar becoming similarly colored and often assuming a definite pinkish tint; conidiophores arising mostly from the substratum, or from aerial hyphae in the deeper colony centers or in floccose strains, mostly 50 to 200μ in length by 2.2 to 3.0μ in diameter, usually unbranched but occasionally bearing one or more branches 25 to 35μ in length, smooth-walled throughout; penicilli typically consisting of a terminal group of 3, 4, or occasionally more, somewhat divergent metulae (fig. $90B_2$) that measure about 12 to 20μ by 2.2 to 3.0μ (apices commonly enlarged to 4.0 or 5.0μ), each supporting a cluster of 6 to 10, more or less crowded and parallel sterigmata measuring about 8.0 to 11.0μ by 2.0 to 2.8μ, and bearing conidia in parallel chains to produce well-defined columns up to 100 to 150μ in length (fig. $90B_1$); conidia globose to subglobose, mostly 2.5 to 3.0μ but ranging from 2.2 to 3.2μ, smooth-walled or nearly so, but often appearing granular when examined in air bubbles.

Colonies on steep agar growing more rapidly, attaining a diameter of 2.5 to 3.0 cm. in 10 to 12 days at room temperature, heavier sporing and more closely furrowed, but in general exhibiting the same basic features as on Czapek; exudate limited to abundant, pale yellow; reverse in yellow to light brown shades; penicilli as described above.

Colonies upon malt extract agar restricted (fig. 92B), rarely exceeding 2.0 cm. in diameter at 10 to 12 days, plane, velvety, heavy sporing throughout, near grayish blue-green (R., Pl. XLVIII), with conidiophores arising from the substratum in a dense stand; no exudate produced; reverse dull yellow to orange. The restricted growth of the species upon this substrate is fairly distinctive and is in marked contrast to the behavior of most Penicillia which produce thin spreading colonies when grown upon malt extract or wort agars.

Species diagnosis based upon the examination of many different strains, of which the following are representative: NRRL 805, isolated in 1940 in Washington as a laboratory contaminant; NRRL 806 (fig. 92A and B), received in 1932 from Professor G. Sabut, Egyptian University, Cairo, Egypt; and NRRL 1842 (fig. 92C and D), received in 1942 from George Smith, London School of Hygiene and Tropical Medicine, as their No. P25.

Our concept of *Penicillium citrinum* Thom is broad in scope and includes forms which vary substantially in particular characteristics, yet possess certain basic features in common. Unquestionably they are inter-related and so belong together. While no exact tabulation has been attempted, it is safe to say that more than 75 per cent of the strains that produce some citrinin and possess penicilli of the *citrinum*-type comply fully with the species description. The remaining related strains can be grouped as follows:

(1) Forms which grow more rapidly and are heavier sporing: Colonies

upon Czapek's solution agar 3.0 to 4.0 cm. in diameter at 10 days, typically velvety, often plane but sometimes showing broad radial furrows, lily green to slate olive in color (R., Pl. XLVII), producing limited pale yellow exudate, and showing colony reverse in dull to fairly bright yellow shades. Colonies upon malt extract agar indistinguishable from those of typical strains. Penicilli are entirely typical. Citrinin is produced. Representative of such forms is culture NRRL 1171, isolated from waste sulfite liquor, and numerous strains, such as NRRL 2143, isolated from deteriorating military equipment in tropical and sub-tropical areas.

(2) Floccose, lightly sporulating strains: Colonies upon Czapek and steep agars typically floccose, loose-textured, up to 2 mm. deep (fig. 92E), penicilli often late in appearing and borne almost exclusively from aerial hyphae, exudate limited, colorless to pale yellow; reverse uncolored to very pale yellow. Colonies upon malt agar are restricted and typical of the species (fig. 92F). Penicilli approximate those of typical strains of *Penicillium citrinum* in form and dimensions of parts. Some citrinin is produced. Represented by NRRL 1841 received in 1942 from George Smith, London School of Hygiene and Tropical Medicine, as "*P. citrinum* Thom No. P6"; and NRRL 2144, isolated by Dr. Richard Baines, California Department of Agriculture, Sacramento, California, from a nylon parachute returned from the South Pacific area.

(3) Forms transitional toward the *Penicillium chrysogenum* series: Colonies upon Czapek's solution agar 3.0 to 4.0 cm. in diameter at 10 days, loose-textured, 1 to 2 mm. deep somewhat floccose, plane or radially furrowed, medium to heavy sporing, court gray to artemisia green (R., Pl. XLVII), exudate pale yellow, and reverse in pale yellow shades. Colonies on malt agar growing more rapidly than on Czapek. Conidiophores are consistently longer than in typical *P. citrinum* strains but penicilli are essentially typical of the species. These forms seem to represent a transitional step between *P. citrinum* Thom and *P. notatum* Westling. Assignment to an intermediate position is substantiated by an apparent capacity to produce both citrinin and penicillin, when tested in spectrum plate cultures against selected bacterial species (L. J. Wickerham, unpublished notes). Representative of these forms is NRRL 822 (Thom No. 4482), received in 1921 from Dr. Frank Forrey from the sputum of a woman with a lung disease.

(4) Forms transitional toward the Monoverticillata: Colonies essentially duplicating typical strains of *Penicillium citrinum* in rate of growth, pattern, texture, spore production and color of conidial surface and reverse; but with conidial structures usually somewhat more variable, and often appearing ramigenous. Conidiophores partly long trailing hyphae, partly short branches from aerial hyphae, and partly erect structures of inter-

mediate length arising from submerged hyphae. Penicilli variously branched or monoverticillate, commonly appearing 2-parted, with terminal and secondary branch equal or unequal in length; not infrequently consisting of terminal verticils of 3 or 4 branches (or metulae) approximately equal in length and withal presenting the picture of typical *P. citrinum*. Represented by NRRL 783 (Thom 5048.14), received in 1929 from Professor Lewis, University of Texas, and NRRL 784, received in 1931 from Dr. H. C. Greene, University of Wisconsin. Thom described *P. sartoryi* n. sp. (1930, p. 233) to cover the general morphology of such forms, emphasizing the branching habit of many of its conidiophores and the abundance of monoverticillate penicilli. He assigned the species to his Monoverticillata-Ramigena and placed it at the end of that group adjacent to the Asymmetrica-Velutina. When tested against selected bacteria in spectrum plate tests, NRRL 783 and 784 were found to produce some citrinin (Wickerham, unpublished notes). This additive evidence of relationship, coupled with the fact that these forms differ from typical *P. citrinum* strains primarily in the production of more irregularly branched and often simpler penicilli, leads us to consider them only as representative of a group of variants within the abundant and cosmopolitan species *P. citrinum* Thom.

(5) Color mutants: Two striking color mutants have been encountered in *Penicillium citrinum* Thom. The first of these, NRRL 2145, was received in July 1945 from Dr. Oswaldo G. de Lima, Recife, Brazil, and is characterized by conidial areas in light tan shades approximating avellaneous to olive buff (R., Pl. XL); colony texture, pattern, rate of growth, and color in reverse are characteristic of the species; penicilli regularly consist of 3 to 6 metulae bearing closely compacted sterigmata and conidial chains in well-defined columns up to 75 or 100μ in length. Colonies on malt agar are restricted and heavily sporing, hence characteristic of the species. When cultures are allowed to incubate at room temperature for 10 to 14 days and are then placed in a cold room there is some tendency to develop green conidia—not as sectors but as a diffuse development throughout the younger conidial areas. Except for the color of its conidia, this strain seems to duplicate NRRL 2143 (see p. 348) in all particulars. It produces a typical citrinin pattern when tested on bacterial spectrum plates.

The second mutant first appeared as a white sector in a colony of NRRL 783 growing on steep agar. Isolated in pure culture, a substrain was obtained which continued to produce colonies characteristic of the parent culture except for a complete lack of conidial color. Structurally the mutant duplicates the parent (see above). The capacity of the mutant to produce citrinin is unimpaired. The mutant is maintained in our Collection as NRRL 783.A.

(6) Nutrient Deficiency Mutants: Cultures are occasionally encountered which grow very sparsely upon Czapek's solution agar but grow luxuriantly, sporulate heavily, and in general duplicate well recognized species upon malt and steep agars. Such a strain of *Penicillium citrinum* has been observed, and the deficiency traced to an inability to utilize nitrate nitrogen. When grown upon substrata containing amino nitrogen this culture developed in a manner typical of *P. citrinum*. It was found to produce citrinin when tested in bacterial spectrum plates. The culture is maintained as NRRL 2148.

Penicillium steckii Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 469–471; Taf. 50. 1927. Thom, The Penicillia, pp. 255–256. 1930.

Colonies on Czapek's solution agar growing rather restrictedly, attaining a diameter of about 2.0 cm. in 10 to 12 days at room temperature, consisting of a close-textured, tough basal felt tearing irregularly, with surface velvety or delicately fibrous, plane or irregularly wrinkled or developing shallow radial furrows in marginal areas (fig. 93A), often more or less zonate with growing margin 1 to 2 mm. wide, thin, white, shading quickly to dull yellow-greens with the development of conidial structures, colonies medium to heavy sporing throughout, approximately gnaphalium green to pea green (Ridgway, Pl. XLVII) or, in age, approaching storm gray (R., Pl. LII), commonly developing limited, more or less flocculent and often sterile, overgrowths in age and showing a marked tendency to develop sectors differing in depth, texture, amount of sporulation; exudate limited to abundant, mostly in small drops, from colorless to very light yellow; odor at first lacking or not pronounced, in age becoming somewhat moldy or sourish; reverse at first colorless or nearly so, often becoming dull yellowish near olive buff (R., Pl. XL) within 2 to 3 weeks; conidiophores abundantly produced, arising from the substratum or the basal felt (fig. 93C), variable in length but usually comparatively short, rarely exceeding 200 to 250μ, commonly less, by 2.8 to 3.3μ, with walls smooth, usually unbranched; penicilli typically biverticillate and consisting of a terminal verticil of 3 to 5 metulae bearing compact clusters of sterigmata (fig. 93D) and well-defined divergent columns of conidia up to 150μ or more in length by 10 to 20μ wide, metulae commonly differing in length, mostly 12 to 15μ by 2.8 to 3.0μ but ranging from 10 to 18μ long; sterigmata in crowded compact clusters, parallel, up to 8 or 10 or more in the verticil, mostly 8 to 10μ by 1.8 to 2.2μ, uniform in diameter except for short, somewhat narrowed conidium bearing tips; conidia globose to subglobose, small, about 2.0 to 2.5μ in diameter, with walls smooth or delicately roughened.

Colonies on steep agar growing somewhat more rapidly than on Czapek,

generally heavier sporing and in somewhat darker shades, similar in texture and basic pattern except for more prominent radial furrows, commonly more or less zonate; exudate and colony reverse as on Czapek; penicilli as described above.

Colonies on malt extract agar comparatively thin, plane, strictly velvety

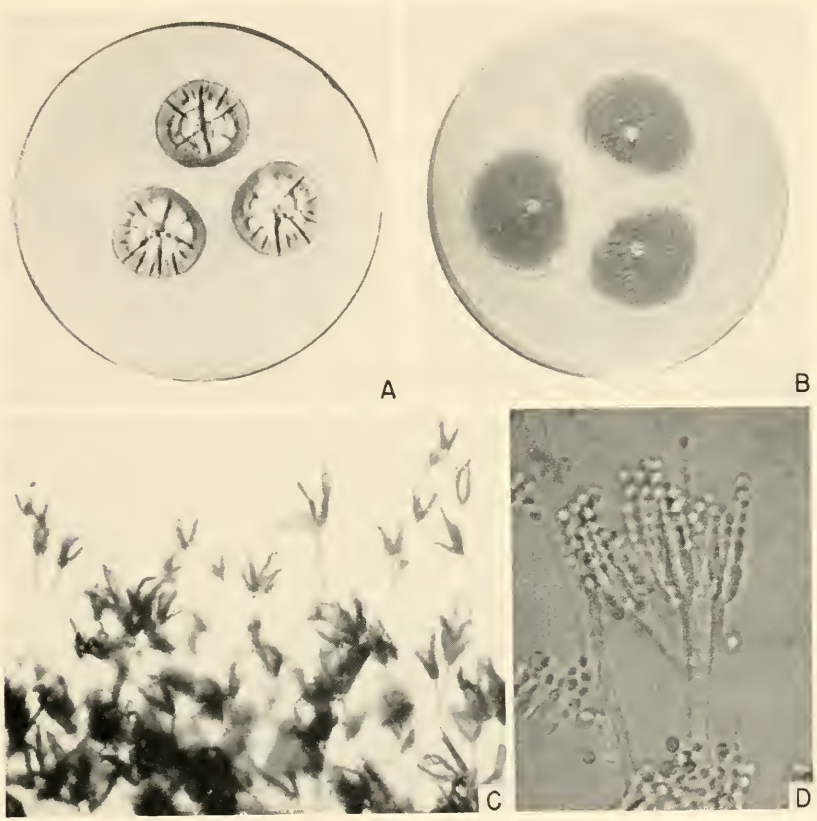


FIG. 93. *Penicillium steckii* Zaleski. *A* and *B*, Two-week-old colonies of NRRL 2141 on Czapek and malt agars. *C*, Low-power view of colony margin in NRRL 2140, × 100. *D*, Detail of penicillus in latter strain, × 750.

(fig. 93B), at first azonate but commonly narrowly zonate in marginal areas after 2 to 3 weeks; exudate lacking; reverse uncolored or nearly so; penicilli as described above.

Species description centered upon NRRL 2140, from Professor Wm. H. Weston as an isolate from a sample of fabric exposed on Barro Colorado Island, Panama; NRRL 2141, from a second sample similarly exposed; and numerous other strains isolated from many different soils and from various

types of military equipment in Panama, Florida, and the southwest Pacific area. The species appears to be widely distributed.

No authentic cultures of *Penicillium steckii* Zaleski have been available for the present study. Thom's culture No. 5010.22, cited as Zaleski's type and discussed in Thom's Monograph (1930, p. 256), was lost from his Collection some years ago. Presumably it is not available from the Centraalbureau, since it was not included among the Penicillia received from them in 1946. Nevertheless, from Zaleski's original diagnosis and figures, and from Thom's subsequent observations on Zaleski's culture, as reported in the latter's Monograph, we believe that *P. steckii* must have represented a form approximating the strains cited above. As understood by us, this species differs from *P. citrinum* Thom primarily in producing colonies with exudate and reverse less highly pigmented, penicilli equally divaricate but somewhat less uniform in pattern, colonies more rapidly growing on malt agar, and an inability to produce the antibiotic citrinin.

Occasional strains are encountered which seem to differ from the above only in their failure to produce well-defined columns of conidia. While identification of such strains may prove somewhat troublesome due to the construction of the key, they are believed to be closely related, hence are assigned to the species *Penicillium steckii* Zaleski as a variant. NRRL 2142, received from Professor Weston as an isolate from exposed fabric in Panama, is representative of such forms.

Occurrence and Significance

Members of the *Penicillium citrinum* series occur upon a wide variety of substrata subject to soil or dust borne contamination including cotton and other fabrics, dairy and food products, tobacco, leather goods, and various vegetable materials undergoing slow decomposition. They occur regularly in soil. They were encountered more frequently than any other Penicillia among the molds isolated from deteriorating military equipment in tropical and sub-tropical areas. They appear to be especially adapted to growth upon leather and woven fabrics under field conditions where such substrata would show great variability in water content. Members of the series are not active cellulose decomposers, nor are they known to rapidly destroy nitrogen rich materials. Their role in decomposition processes, if it is substantial, probably resides in their ability to gain an early foothold and so prepare the way for the invasion of more destructive forms. Not infrequently they occurred upon lens mountings, with the hyphae extending out upon the glass surface and etching it sufficiently to render it unserviceable.

Hetherington and Raistrick (1931b) reported the production from glucose of a yellow coloring matter, citrinin, by strains of *Penicillium citrinum* Thom. Cultures were grown in Czapek-Dox nutrient broth and the material obtained in crystalline form by acidification and subsequent cooling of the metabolism solution. Citrinin, $C_{13}H_{14}O_5$, was found to be a laevorotatory (in alcohol) monobasic acid which melted at 166–170°C., was virtually insoluble in water, but readily soluble as the sodium salt. Coyne, Raistrick, and Robinson (1931) made a detailed study of the chemistry of citrinin and proposed a structural formula. The validity of this formula was subsequently questioned by Gore, Panse, and Venkataraman (1946) and by Sprenger and Ruoff (1946), who presented experimental evidence in support of their conclusions.

Raistrick and Smith (1941) reported metabolism solutions of *Penicillium citrinum* to have antibiotic properties and attributed this to their citrinin content. Oxford (1942a) investigated this more carefully and found citrinin to have a selective action against Gram-positive bacteria, although some Gram-negative forms were inhibited in low dilutions. The antibiotic is too toxic to be of wide usefulness. Ambrose and De Eds (1945) found doses of 50 mg./kg. of body weight to be toxic to mice, rats, and guinea pigs when administered parenterally. Chu (1946), however, reported the sodium salt of citrinin to produce little irritation when applied to the skin or mucous membranes of animals and man.

The production of citrinin is typical of *Penicillium citrinum* Thom, and this biochemical characteristic can be advantageously used in identifying miscellaneous isolates or accessions as already noted (see p. 69). The production of citrinin is not, however, limited to this species as Raistrick and Hetherington originally believed (1931). Raistrick and Smith (1935) reported citrinin from one of five strains of *Aspergillus terreus* studied. Timonin (1942) and Timonin and Rouatt (1944) employed a white-spored *Aspergillus* for citrinin production, and obtained substantially greater yields than with strains of *P. citrinum*. The culture was reported as belonging to the *A. candidus* group but was found to represent *A. niveus*, one of the *A. terreus* group, when examined by us. Using the same culture, Wylie (1945) reported citrinin yields up to 4.5 gm./liter culture solution in 10 days, or 5.5 gm./liter in 15 days. Ewart (1933) had earlier isolated citrinin from *Crotalaria crispata*, reporting yields of 1–1.2 per cent in the dried leaves of this flowering plant from tropical North Australia.

Nandi (1945) reported the production of an antibacterial substance from a strain of *Penicillium citrinum* isolated in Calcutta. Identity with citrinin is possible.

In a survey of the production of acids from glucose by fungi, May, Her-

rick, Thom, and Church (1927) found gluconic and citric acids to be produced in varying amounts by strains of *Penicillium citrinum*.

Cavallito (1944) isolated 1.1 to 1.3 per cent ergosterol from the mycelium of *Penicillium citrinum*, and slightly lesser yield from *P. chrysogenum*.

Penicillium citrinum has been isolated from lungs and respiratory infections, but actual pathogenicity has not been proved. In a single case the species was isolated from macroscopic masses of hyphae passed in the urine of a patient with renal colic.

Utilization of various C and N sources by *Penicillium citrinum* was studied by Bailey and Cavallito (1944). Sugars and sugar alcohols afforded better sources of carbon than their acids; and nitrate and ammonium salts were utilized better than amino, amide, imide, or nitrite nitrogen.

Penicillium citrinum is one of the common causes of "fungus fouling" of optical instruments in tropical areas through growth of the hyphae on lenses and prisms. Vicklund (1946) incorporated radium sulphate in a metallic foil surrounding glass parts, and reported satisfactory control without risk to users. The fungistatic effect was due to alpha radiation.

Pénau, Levatidi, and co-workers (1943 to 1945) investigated an antibiotic substance, termed corylophilin, produced by *Penicillium corylophilum* Dierckx. Production and isolation of corylophilin was reported by Pénau and Hagemann (1943b) and Pénau, Levatidi, and Hagemann (1943c). Perault and Greib (1944) discussed its mode of action and observed that it was bactericidal only in the presence of glucose, and that bacteria were killed by the evolution of H_2O_2. There is reason, therefore, to believe that corylophilin is identical with notatin which is produced by *P. notatum* under acid conditions in the presence of glucose. Some question exists regarding the validity of their species identification, in fact, Pénau *et al.* (1943a), in their original paper, noted that the mold under study resembled *P. notatum*. There are reasons to believe that it probably represented this species.

Mull, Townley, and Scholz (1945) reported the production of gliotoxin and a second antibiotic substance by a *Penicillium* identified in 1945 by one of us (K. B. R.) as "suggesting *P. obscurum* Biourge but showing globose rather than elliptical conidia." More recent examination of this culture in comparison with different species in the Monoverticillata and the *P. citrinum* series shows it to represent a strain of *P. terlikowskii* Zaleski approximating in appearance the culture found by Brian (1946) to produce gliotoxin.

Mallman and Michael (1940a and b) reported *Penicillium chloro-leucon* Biourge (see p. 345), and *P. puberulum* as the two Penicillia most commonly found within cold storage eggs.

Penicillium chrysogenum Series

Outstanding Characters

Colonies typically velvety, ranging from close to loose-textured in appearance, with conidiophores usually arising in a dense stand from the substratum or a basal felt; in some strains more or less floccose, with conidiophores borne as branches from aerial hyphae; usually characterized by conspicuous furrows forming a radiate or wheel-like pattern.

Colonies generally characterized by abundant exudate, often collecting into conspicuous droplets, ranging in color from light to rich yellow.

Colony reverse usually in shades of yellow, commonly becoming brown in age, with surrounding agar usually yellow in color, often conspicuously so.

Penicillus asymmetrical, smooth-walled throughout, irregularly branched in larger structures, or commonly consisting of a terminal verticil of metulae in smaller fruits; often characterized by well-defined columns of conidia that arise from individual verticils of sterigmata, which when viewed separately appear almost as monoverticillate structures.

Conidia smooth-walled, varying from globose to subglobose in some forms to definitely elliptical in others, and ranging in size from approximately 2.5 to 4.0μ or 4.5μ in diameter.

Series Key

1′. Conidia elliptical, or occasionally subglobose.
  aa. Colonies usually showing abundant yellow exudate and yellow pigmentation in reverse ..... *P. chrysogenum* Thom
  bb. Colonies showing pale or colorless exudate, and vinaceous to brownish fawn colors in reverse ..... *P. meleagrinum* Biourge

2′. Conidia globose to subglobose.
  aa. Colonies velvety, heavily sporing, in rich blue-green shades, often comparatively thin ..... *P. notatum* Westling
  bb. Colonies loose-textured, flocculent, often lightly sporing, comparatively deep ..... *P. cyaneo-fulvum* Biourge

The members of this series are especially common in nature and regularly occur in soil and upon a wide variety of organic substrata. They have received much detailed study during the past few years because of their capacity to produce the antibiotic penicillin (see Chapter V).

Members of the series as isolated from nature are quite variable in pigmentation, exudate formation, colony texture, rate of growth, etc., yet all show the general features indicated above and can be readily recognized.

Cultures long maintained in the laboratory may remain quite stable and reduplicate, year after year, their original cultural and morphological characteristics. Or they may undergo progressive variation, and in a relatively short time evolve or degenerate into flocculent and lightly sporulating forms

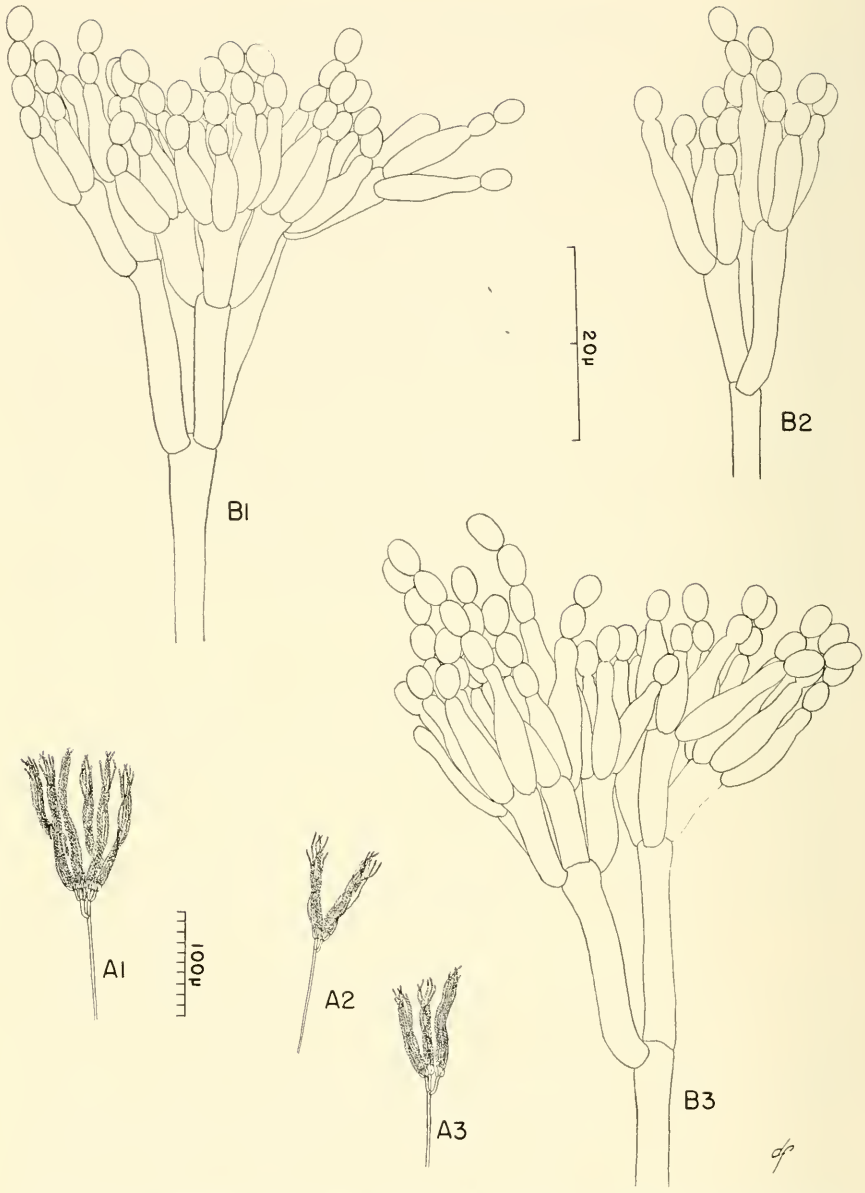


FIG. 94. *Penicillium chrysogenum* Thom. A_1–A_3, Habit sketches of representative penicilli showing conidial chains arranged in characteristic columns. B_1–B_3, Camera lucida drawings of representative penicilli showing details of cellular structure, and variations in pattern and complexity.

that hardly resemble the original, yet retain sufficient of their characteristics to counter-indicate any possibility of contamination or replacement by foreign strains.

In the morphology of the penicillus, members of the series vary from strains in which the separateness of individual verticils gives the effect of a fertile hypha bearing a series of branches with each producing a monoverticillate conidial mass, to a complex and typically asymmetrical conidial apparatus (fig. 94). The conidia vary from globose to subglobose, and from quite small, as in typical strains of *Penicillium notatum* with diameters mostly less than 3.5μ, to strains of *P. chrysogenum* with conidia 4.0 to 4.5μ in long axis and definitely elliptical.

It is quite impossible to draw any sharp lines of separation within the *Penicillium chrysogenum* series due to the prevalence of intergrading strains. Satisfactory definition of species, therefore, becomes extremely difficult, and recognition of a particular culture as representing this species or that, must rest ultimately upon the judgment and experience of the individual worker. Thom (1930) listed nine species as belonging to this series, which he termed the Radiata, after a prior usage by Biourge (1923), and cited individual strains as more or less adequately satisfying the description of each. Most of these had come recently from Biourge and represented the type material for species published by him or his predecessor, Dierckx. Many of them are still in our possession and in general continue to exhibit the characteristics noted for them two decades ago. In the meantime, however, hundreds of new isolates have been examined, including many intergrading forms. We are compelled to conclude that Biourge (1923) and Dierckx (1901) described their species largely upon individual strains which represented contrasting forms in a series for which intergrading individuals were not then known.

While it is extremely difficult to define a species in this series, it is obvious that all strains belonging to it cannot be regarded as representing a single species, for many of them differ greatly from one another in almost any character selected as a basis for comparison. Based upon careful, and in some cases exhaustive, study of hundreds of strains belonging to this series during the past few years, we believe a separation into four species will prove reasonably practicable. The species so recognized, together with their salient characteristics, are as follows:

Penicillium chrysogenum Thom, marked by heavy sporing, velvety, often rather loose-textured colonies in blue-green to yellow-green shades; comparatively large and often rebranched penicilli, with the conidial chains arising from individual metulae usually adhering into fairly well-defined columns, and with conidia regularly elliptical and fairly large, up to 4.0 to 4.5μ in long axis.

Penicillium meleagrinum Biourge, marked by rapidly growing, loose-textured, heavily sporing colonies with conidial areas in bright yellow-green shades, exudate pale or uncolored, reverse in dull yellow to vinaceous or brownish fawn shades; penicilli comparatively large and often rebranched; and conidia comparatively large and elliptical.

Penicillium notatum Westling, marked by heavily sporing, velvety colonies, often appearing close-textured; penicilli smaller than above, commonly consisting of a single verticil of metulae; conidia globose to subglobose, usually smaller in size.

Penicillium cyanco-fulvum Biourge, marked by less heavily sporing colonies that are deeper and of looser texture, light blue-green to gray-green in color, exudate and colony reverse often in light yellow shades; penicilli variable in size and pattern and often irregular; and conidia globose to subglobose, variable in size, in some strains comparatively large up to 4.0μ or more.

This latter species is recognized to include a number of loose-textured, lightly colored forms which produce pale or limited exudate, and generally show reduced pigmentation in colony reverse and in the surrounding agar. It is possible that such forms may appear as cultural variants of *Penicillium notatum* or *P. chrysogenum*. Whatever their origin, several of them have been held as laboratory cultures for many years. Forms of this type are isolated from nature with sufficient frequency to necessitate recognition of a species to which they can be assigned.

It is clearly recognized that workers in the laboratory will often encounter difficulties in assigning particular strains to one or the other of the above species, for cultures showing the character of more than one "species" are repeatedly encountered. Individual cultures when grown side by side in cultures often show marked differences in gross appearance, only to have such distinctions slip away and blend into the picture of a variable and inconstant series when great numbers of strains are examined. Furthermore, the same strain may show marked differences in habit, texture, and coloration depending upon the particular substratum and other specific factors of environment. Speaking of the type strain of *Penicillium chrysogenum* (Thom's No. 26—NRRL 807) Thom, in 1930, wrote as follows:

> "Re-examination of records of observations over the twenty-two years this species has been kept in culture shows as great a range in color in the various recorded experiments as is shown by the whole series of Radiata."

An additional twenty year study of this and other cultures has tended to enhance the significance of this observation. Nevertheless, specific stains generally do possess definite individuality, either cultural, morphological, or physiological in character. These, the experienced mycologist or micro-

biologist soon comes to recognize so that valuable strains can be maintained without great difficulty.

Members of the *Penicillium chrysogenum* series appear to be unusually long-lived. Thom (1930) reported a culture as viable after 8 years in a laboratory test tube. In a series of viability tests made in 1945 on test-tube cultures that had been brought to Peoria five years earlier, members of this series, almost without exception, were still viable and produced colonies characteristic of the various strains tested. This was not equally true of any other series of the Penicillia. It was approached only by the *P. purpurogenum* and *P. funiculosum* series in the Biverticillata-Symmetrica where approximately 50 per cent remained viable. As a matter of fact, the longevity of conidia in dry test-tube cultures has upon occasion provided valuable indications of true relationships in isolated cases where strains had been incorrectly diagnosed.

The separation here proposed is far from ideal, but it is believed to be workable in the vast majority of cases. Fortunately, for many types of investigation, including the search for improved penicillin producing molds, identification to the series is sufficient—high yielding strains may belong to either *P. notatum* or *P. chrysogenum*. The species selected for recognition can be expected to serve principally as guide-posts in a great series of intergrading strains. Seldom will they offer the worker assurance that he has rediscovered the exact organism described by an earlier investigator.

Penicillium chrysogenum Thom, in U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, pp. 58–60, fig. 20. 1910; Thom, The Penicillia, pp. 261–262. 1930. See also Biourge, Monograph, La Cellule **33:** fasc. 1, pp. 170–172, Col. Pl. IV and Pl. VI, fig. 32. 1923; and Westling, Arkiv f. Bot. **11:** 54, 107–108, figs. 23 and 64. 1911.

Colonies on Czapek's solution agar growing rapidly, attaining a diameter of 4.5 to 5.0 cm. in 10 to 12 days at room temperature, consisting of a comparatively thin basal felt bearing crowded conidial structures, in some strains closely velvety (fig. 95A), in others deeply velvety and rather loose-textured (fig. 95E), usually azonate, typically showing conspicuous radial furrows which lend to the colony a wheel-like appearance, comparatively deep, up to 1 mm. or more in some strains, thin in others, not exceeding 300–500μ, with growing margin 1 to 2 mm. wide, white; heavily sporing throughout in most strains, in others often showing some tendency to remain sterile in central areas with vegetative mycelium yellowish to cream colored, conidial areas in yellow-green to bluish gray-green shades, in some strains ranging from pistachio green to American green (Ridgway, Pl. XLI) becoming blue-green near Russian green or dark Russian green (R., Pl.

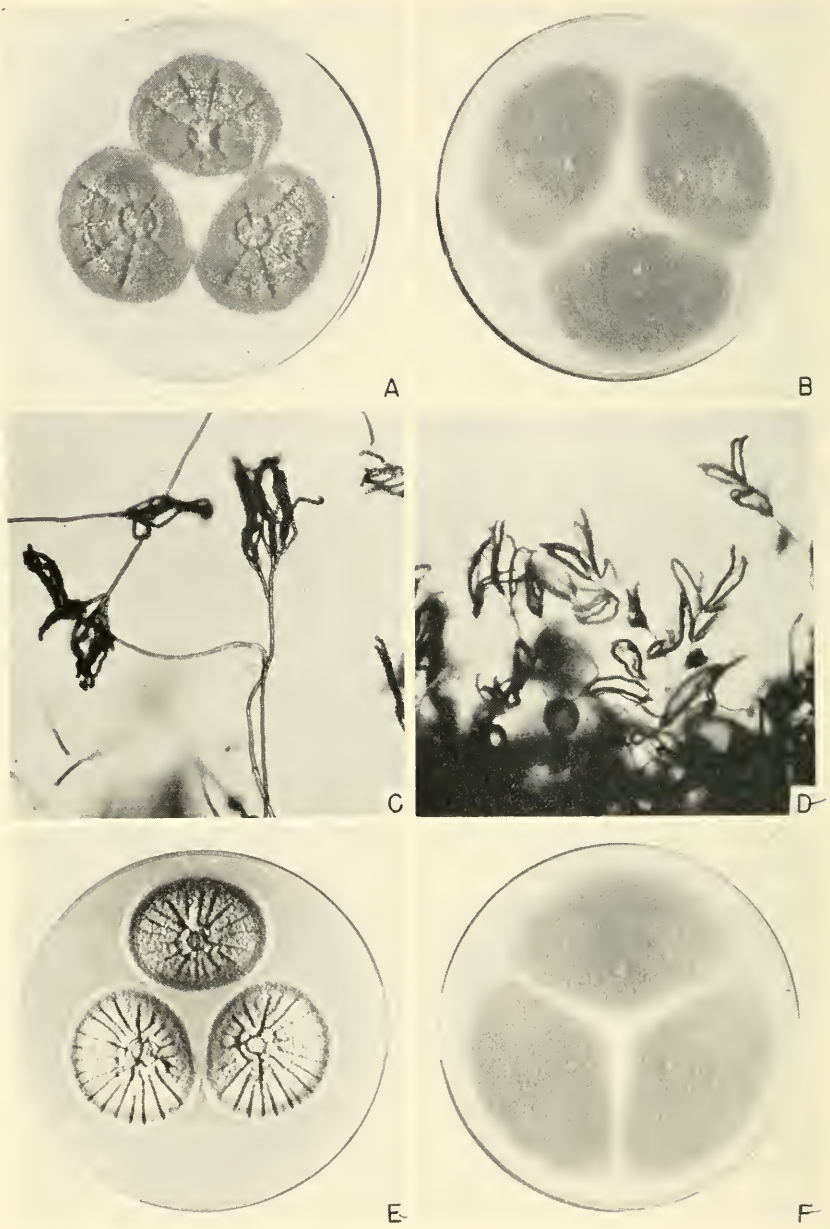


FIG. 95. *Penicillium chrysogenum* Thom. *A* and *B*, Two-week old colonies of strain NRRL 807 (type) on Czapek and malt agars. *C*, Penicilli of same strain seen under a high-dry lens, × 165. *D*, Low-power view of colony margin in NRRL 1951, showing characteristic columns of conidia, × 80. *E* and *F*, colonies of the latter strain on Czapek and malt agars at two weeks.

XLII) after two or three weeks, in others ranging from celandine green through artemisia green to lily green (R., Pl. XLVII) or deep bluish gray-green (R., Pl. XLII); exudate abundantly produced in most strains, collecting as conspicuous droplets (fig. 95A), in light to citrine yellow shades; odor lacking or indefinite; reverse bright yellow near strontian yellow (R., Pl. XVI) to dull yellow shades near olive-yellow (R., Pl. XXX), with surrounding agar usually colored throughout in lighter tints of the same shades. Conidiophores arising primarily from the substratum in a dense stand, variable in length, commonly up to 150 to 350μ or more in length by 3.0 to 3.5μ in diameter, with walls smooth and colorless; penicilli biverticillate and asymmetrical, commonly showing one or more branches in addition to the main axis (fig. 94B) terminating in verticils of 2 to 5 metulae bearing sterigmata; conidial chains usually in well-defined columns commonly up to 200μ in length (fig. 94A and 95D); branches variable, commonly 15 to 25μ in length by 3.0 to 3.5μ in diameter; metulae usually 10 to 12μ by 2 to 3μ, occasionally longer; sterigmata in fairly compact verticils of 4 to 6, mostly 8 to 10μ by 2.0 to 2.5μ but variable in different strains, with conidium-bearing tips somewhat narrowed; conidia elliptical, rarely subglobose, mostly 3.0 to 4.0μ by 2.8 to 3.5μ, occasionally larger, smooth-walled, yellowish green in mass.

Colonies on steep agar growing more rapidly, 5.5 to 6.0 cm. in 10 to 12 days, strictly velvety, with conspicuous radial furrows, heavily sporing throughout except for a narrow white to yellowish growing margin 1 to 2 mm. wide, conidial areas showing the same colors as on Czapek's agar; exudate as described above but often more abundant; reverse in yellow shades, usually somewhat duller than on Czapek; conidial structures as described above but with columns often longer up to 300μ or more.

Colonies on malt agar, 5.5 to 6.0 cm. in 10 to 12 days, plane (fig. 95B and F), never furrowed, strictly velvety, conidial areas showing the same colors as above; exudate lacking; reverse in dull yellowish shades; conidial structures as described above.

Species diagnosis centered upon Thom's description based on the type strain, NRRL 807 (Thom's No. 26), and upon comparative examination in culture of many additional strains presenting the same basic cultural and morphological characteristics. Strains now contained in our Collection which are regarded as typical of the species include: NRRL 812, received in 1940 from Professor H. Hotson, University of Washington, Seattle, as an isolate from a 4 per cent iron-alum solution; NRRL 1186, received in 1940 from Dr. G. A. Ledingham, Ottawa, Canada as an isolate from meat brine; NRRL 838, received in 1931 from Professor A. W. Henry, University of Alberta, Edmonton, Canada; NRRL 811, received in 1921 from Dr. J. H. Birkinshaw, Nobels Explosives Co., Ayrshire, Scotland as an

isolate from tobacco; NRRL 1951, isolated at this Laboratory in July, 1943, from a cantaloupe; and many others. NRRL 843, from the Biourge Collection, through Dr. Paul Simonart in 1936, differs from the above in producing larger and strongly elliptical conidia ranging up to 4.5 or 5.0μ in long axis.

All of the cultures listed above produce fair to good yields of penicillin in both surface and submerged cultures. NRRL 1951 is of special interest since it represents the stock from which such high penicillin-yielding natural variants as NRRL 1951.B25, and the artificially induced mutations X-1612 and Wis. Q-176 were obtained (see pp. 96–98). NRRL 811 is also of special interest since it represents the first culture which May, Herrick, *et al.* successfully adapted to the production of gluconic acid by submerged culture techniques (May, *et al.*, 1934 and Moyer, *et al.*, 1936).

The species is unusually common in nature and shows the same general distribution as listed for the series (see p. 373).

The species *Penicillium chrysogenum* Thom, in a broad sense, includes a number of fairly well-defined cultural aspects. These differ from one another enough to be recognized, but fail to develop sufficient differences to warrant specific or varietal separation. The following strains are representative of some of these cultural types:

NRRL 807, the type strain, originally produced fairly loose-textured, radially furrowed colonies that were heavily sporing and strictly velvety throughout, and developed comparatively large, often rebranched penicilli bearing elliptical conidia about 4.0μ in long axis. After forty years of continuous laboratory cultivation the details of fruiting structures remain essentially unchanged, but colonies now tend to be more restricted, somewhat flocculent in central areas, and usually develop a comparatively thin, heavily sporulating but closely velvety marginal zone. Pigmentation of conidial areas and of colony reverse remain unaltered.

NRRL 1951, cited above as a typical strain, produces comparatively deep, loose-textured, radially but not deeply furrowed, velvety colonies that are heavily sporing throughout, and develop very large, usually rebranched penicilli with strongly elliptical conidia. Exudate formation is often somewhat reduced and pigmentation in colony reverse is less marked than in the type preceding. Natural variants separated from this basic stock by experimental techniques cover almost the entire gamut of cultural types seen in the *Penicillium chrysogenum* series (Raper and Alexander, 1945b).

NRRL 1984, a good penicillin producing strain (see p. 100), produces colonies strikingly like NRRL 807 above except for a reduction of sterile mycelia in central colony areas; penicilli are of the same general dimensions and pattern, but conidia are mostly globose to subglobose as in *Penicillium*

notatum Westling. The strain is regarded as somewhat transitional in the direction of that species.

NRRL 843, cited above as a large-spored form, differs from such loose-textured strains as NRRL 1951 principally in producing conidia of larger dimensions. This strain is believed by us to have approximated the kind of culture upon which Westling based his species *Penicillium baculatum*.

NRRL 792, received from Biourge as the type of his *Penicillium rubens*, represents a rapidly spreading, prominently furrowed, loose-textured form, producing conidial areas in rather bright yellow-green shades, penicilli that are loosely constructed and sometimes almost divaricate, and strongly elliptical conidia. Culturally this strain is somewhat suggestive of *P. cyaneo-fulvum* Biourge.

NRRL 889, received from Biourge as representing his type of *Penicillium roseo-citreum* (see p. 364), produces lightly furrowed, deeply lanose to flocculent colonies 2–4 mm. deep which show the general cultural characteristics of the Lanata section but produces abundant yellow exudate and pigmentation, develops asymmetric penicilli typical of the present series, and upon suitable substrata produces some penicillin. This strain and others approximating it are regarded as possibly transitional toward *P. cyaneo-fulvum* Biourge.

Species described by other authors which are regarded as either approximating *Penicillium chrysogenum* Thom, or to be inseparable from it include the following:

Penicillium baculatum Westling (Svensk Botanisk Tidskrift **4:** 139–145, text figures 1–3. 1910; see also Arkiv för Botanik **11:** 53, 79–83, figs. 11 and 53. 1911. Compare Biourge, Monogr., La Cellule **33:** fasc. 1, pp. 186–188; Col. Pl. IV and Pl. VII, fig. 40. 1923; and Thom, The Penicillia, pp. 268–269. 1930) was described originally as an ascosporic species producing lenticular ascospores 4.2 to 4.8μ by 5.2 to 6.0μ. Thom received two cultures under this name from Westling, from the second of which a strain of *Aspergillus repens* was isolated by adding high percentages of sugar to the culture. There is reason to believe that the perithecia observed and described by Westling belonged to this *Aspergillus*. The *Penicillium* present in each of the two cultures belonged to the group with *P. chrysogenum* Thom. Westling's organism appears to have been somewhat looser-textured than most, and to have produced large conidia with more pronounced ellipticity, probably approximating NRRL 843 listed above among the strains representative of *P. chrysogenum*. Otherwise, the culture probably represented a typical strain of Thom's species, and *P. baculatum* is regarded as synonymous with this well recognized form.

Penicillium chlorophaeum Biourge (Monogr., La Cellule **33:** fasc. 1, pp. 271–273; Col. Pl. VIII and Pl. XIII, fig. 78. 1923. Thom, The Penicillia, pp. 262–263. 1930) as known from Biourge's type, reported by Thom in 1930 as No. 4733.31 and now maintained as NRRL 817, represents a form producing comparatively deep, loose-textured, velvety to almost lanose, lightly sporulating colonies light blue-green to gray-green in color, producing abundant colorless to light tan exudate, and with re-

verse and agar in dull yellow to light orange or brown shades. Penicilli are somewhat irregular, often comparatively large, and consist either of a terminal verticil of metulae only, or the main axis and one or more branches bearing metulae and sterigmata; sterigmata mostly in groups of 3 to 5 with conidial chains tangled or forming poorly defined columns; conidia are globose to broadly elliptical, smooth-walled, about 3.4 to 3.8μ by 3.0 to 3.5μ. The above notes conform fairly closely with Biourge's original description but fail to furnish sufficient bases for separation from *P. chrysogenum* Thom when one considers the various cultural aspects that this species is known to present.

Penicillium fluorescens Laxa nomen nudum (?) was cited but not described by Laxa, Zentbl. f. Bakt. etc. (II) **86:** 164–165. 1932. A culture received from him in March 1933 and now maintained as NRRL 819, is regarded as representing a cultural variant of *P. chrysogenum* Thom in which the surface and reverse of the colony on Czapek's solution and steep agars are marked by conspicuous dendroid, rather than strictly radial, furrows. The colony surface is comparatively loose, almost floccose and little or no exudate is produced; colony reverse and surrounding agar are in bright yellow shades. Conidial structures are like those of a light sporing strain of *P. chrysogenum*. The culture produces little penicillin.

Penicillium roseo-citreum Biourge (Monogr., La Cellule **33:** fasc. 1, pp. 184–186; Col. Pl. IV and Pl. VII, fig. 39. 1923) as originally described and as represented by Biourge's type strain, discussed by Thom in 1930 as No. 4733.106 and now maintained as NRRL 889, apparently represents a deeply floccose member of the *P. chrysogenum* series. Thom (1930, p. 323) included this species in his section Lanata upon the basis of the colony texture. Pigmentation, exudate formation, and the pattern of its penicilli, however, indicate closer relationship to the series indicated above. The type culture is regarded as probably representing a floccose variant of *P. chrysogenum* Thom. The culture produces some penicillin. A strain received from the Centraalbureau as *P. citreo-roseum* (to them from Biourge in 1927) duplicates NRRL 889.

Penicillium rubens Biourge (Monogr., La Cellule **33:** fasc. 1, p. 265; Col. Pl. XI and Pl. XIX, fig. 111. 1923. Thom, The Penicillia, pp. 249–250, fig. 33. 1930) as known by the type strain, discussed by Thom in 1930 as No. 4733.110 and now maintained as NRRL 792, represents a member of the *P. chrysogenum* series, hardly separable from *P. chrysogenum* Thom. The strain produces comparatively loose-textured colonies with central areas more or less flocculent and marginal areas medium to heavy sporing in rather bright yellow-green shades; exudate is limited and pale yellow in color; colony reverse is at first in bright yellow shades, becoming dull in age; penicilli are comparatively loose, often consist of a terminal verticil of metulae, and bear conidia mostly elliptical and about 3.5μ in long axis. The culture produces some penicillin.

Penicillium meleagrinum Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 147–149; Col. Pl. III and Pl. IV, fig. 22. 1923. Thom, The Penicillia, pp. 266–267. 1930.

Colonies on Czapek's solution agar growing rapidly (fig. 96A), attaining a diameter of 4.5 to 5.0 cm. in 12 days at room temperature, consisting of a fairly tough basal felt bearing abundant conidial structures, central colony area commonly non-sporulating or lightly sporulating, near cream in color,

becoming deeper in submarginal area up to 1 mm. or more, sometimes almost flocculent, strongly furrowed in a radial pattern, heavily sporing, loose-textured, velvety, with marginal zone about 0.5 to 1.0 cm. wide, plane, heavily sporing, strictly velvety, with conidial structures arising directly from the substratum, conidial areas in greenish glaucous shades from pis-

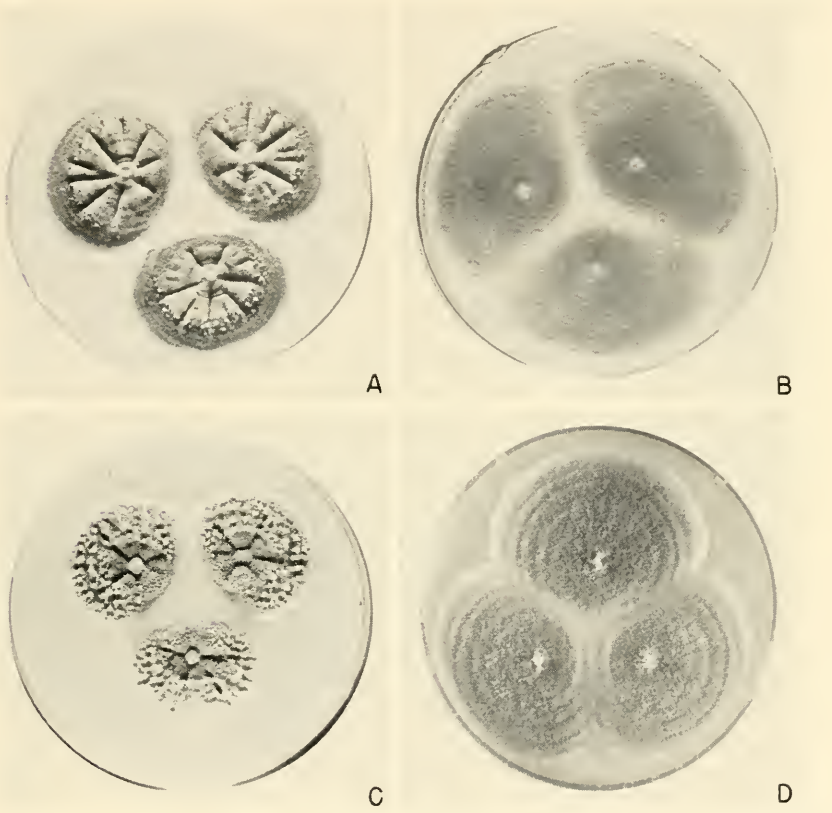


FIG. 96. *A* and *B*, *Penicillium meleagrinum* Biourge, NRRL 2136, on Czapek and malt agars at two weeks. *C* and *D*, *P. cyaneo-fulvum* Biourge, NRRL 837, as above.

taschio green (Ridgway, Pl. XLI) to Russian green (R., Pl. XLII), growing margin broad, thin, white, 1 to 3 mm. wide, with outermost portion largely submerged, gradually developing conidial structures; exudate fairly abundant, in small droplets, pale yellow, often largely embedded and sometimes overgrown to give a tufted appearance; odor fruity or spicy, not pronounced; reverse in dull yellow to vinaceous or brownish drab shades (R., Pl. XLV) with surrounding agar usually uncolored; conidiophores smooth-walled arising primarily from the substratum, mostly 200 to 250μ by 2.8 to

3.3μ less commonly 400 to 500μ in length occasionally borne from aerial hyphae and shorter, about 50 to 75μ in length, apices somewhat inflated; penicilli asymmetric, commonly branched, with branches and main axes each usually bearing 2 to 4 metulae to form a fairly large conidial structure, less commonly consisting of a simple terminal verticil of metulae only, with conidial chains adherent into fairly well-defined columns up to 150μ in length, branches when present variable, from 10 to 20μ by 2.0 to 3.0μ; metulae mostly 9 to 12μ by 2.0 to 2.5μ; sterigmata closely appressed, in compact clusters of 6 to 8, about 7 to 9μ by 1.8 to 2.2μ; conidia elliptical, 3.0 to 3.5μ by 2.5 to 3.0μ, smooth-walled, light yellow-green.

Colonies on steep agar growing more rapidly, about 5.5 to 6.0 cm. in 12 days, comparatively loose-textured, velvety, conspicuously and closely radiate in pattern, heavily sporing throughout, with conidial areas colored as above; exudate abundant, clear or nearly so, in small droplets, with craters resulting from evaporation appearing pinkish; reverse in vinaceous drab shades, penicilli as described above except conidiophores averaging somewhat longer.

Colonies on malt agar spreading broadly, about 6.0 to 6.5 cm. in 12 days, plane (fig. 96B), strictly velvety, near Russian green (R., Pl. XLII); no exudate produced; reverse uncolored or in dull yellow shades; penicilli as described above but with well-defined columns up to 200 to 250μ in length.

Species description centered upon NRRL 836, received in January 1929, from J. H. Birkinshaw, Nobel Explosives Company, Ayrshire, Scotland and discussed by Thom (1930) under this name as No. 5034.53 in 1930; NRRL 2136, received in September 1943, from Nancy Atkinson, Institution of Medical and Veterinary Science, Adelaide, Australia, as an unidentified *Penicillium* reported to produce an antibiotic similar to penicillin; and a few additional cultures duplicating the above but not maintained in our permanent collection. The species appears to represent a widely distributed but fairly uncommon soil form.

Tests conducted at this Laboratory show that cultures of the present type produce limited amounts of penicillin.

Biourge described *Penicillium meleagrinum* as characterized by an aerial down and spotted colony reverse, presenting a guinea hen appearance, from which character the name is derived. Thom (1930) recognized under this name cultures obviously belonging to the *P. chrysogenum* series which showed broad white growing margins, reddish, violaceous or drab colored reverse, clear exudate, asymmetrical smooth-walled penicilli, and elliptical smooth conidia 3.0 to 3.5 or 4.0μ in long axis. Exact duplication of Biourge's species was not claimed, since his type had not been seen. In neither exudate nor colony reverse does the species show the bright yellow colors that are generally characteristic of the present series. Recognition

of a species, as described above, is necessary, however, to include strains with obvious relationships here which show the several characters recognized by Thom and attributed to *P. meleagrinum* Biourge.

Penicillium notatum Westling, in Arkiv för Botanik **11:** 55, 95–97, figs. 17, 59. 1911. See also Biourge, Monograph, La Cellule **33:** fasc. 1, pp. 179–181, Col. Pl. IV and Pl. VIII, fig. 37. 1923. Thom, The Penicillia, pp. 264–265. 1930.

Colonies on Czapek's solution agar growing fairly rapidly in most strains (fig. 97A, C, D, and F), attaining a diameter of 3.5 to 4.0 cm. in 10 to 12 days at room temperature, in some strains more restricted (fig. 97E), not exceeding 2.5 to 3.0 cm., consisting of a fairly close-textured basal felt bearing abundant conidial structures, commonly azonate, usually showing conspicuous radial furrows to produce a wheel-like appearance, heavily sporing throughout except for a white to yellowish growing margin 1 to 2 mm. wide in most strains, in others rather light-sporing and yellowish in colony centers; conidial areas in blue-green shades usually ranging from celandine through artemisia to lily green (Ridgway, Pl. XLVII), in some strains becoming darker near Russian green to deep bluish gray-green (R., Pl. XLII) to slate olive in age; exudate abundantly produced in most strains, often collecting in large drops, 2 to 3 mm. in diameter, clear yellow to light amber in color, tending to reduce spore production and markedly affecting the overall colony appearance; odor not pronounced; reverse yellow to golden yellow, commonly becoming light brown in age, with the pigment diffusing throughout the substratum; conidiophores arising primarily from the basal felt, variable in length from 250 to 500μ by 2.5 to 3.0μ in some strains or 3.0 to 3.5μ in others, with walls smooth and colorless; penicilli biverticillate, sometimes showing one or more fertile branches but commonly consisting of a simple terminal verticil of metulae bearing clusters of sterigmata (fig. 98A and C), and conidial chains up to 50–75μ in length, tangled or adherent into fairly well-defined columns; branches, when present, variable in size, mostly 10 to 15μ by 2.5 to 3.0μ; metulae usually in groups of 3 to 5, variable in length, ranging from 9 to 16μ by 2.5 to 3.0μ but commonly 10 to 12μ in length; sterigmata commonly borne in verticils of 4 to 6, mostly 8 to 10μ by 2.0 to 3.0μ, terminating rather abruptly; conidia globose to subglobose, mostly 3.0 to 3.5μ in diameter, less commonly showing some ellipticity, smooth-walled, yellowish green in mass.

Colonies on steep agar growing somewhat more rapidly but similar to the above in general pattern and texture, strictly velvety, heavily sporing throughout, usually in slightly darker shades, conspicuously furrowed in a radial pattern; exudate abundantly produced; odor lacking or indefinite; reverse and agar in duller shades than on Czapek's agar, near deep colonial

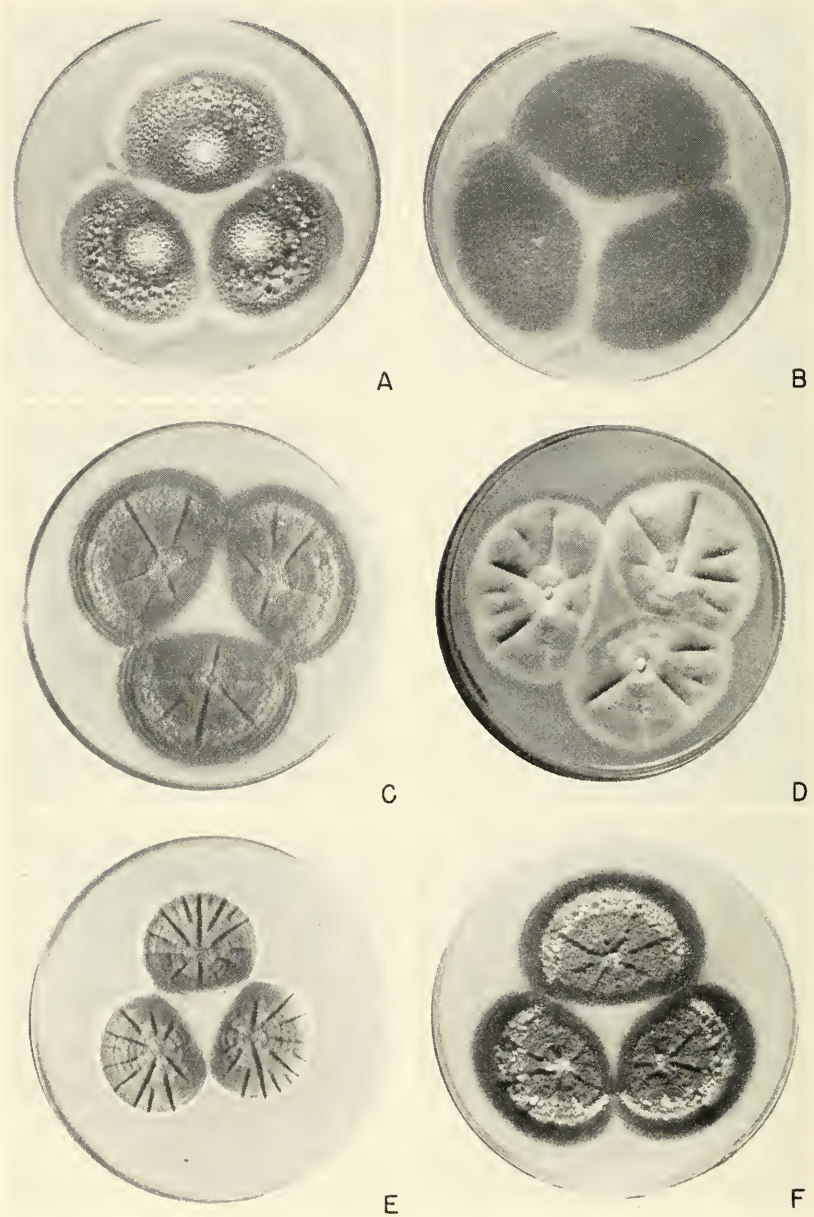


FIG. 97. *Penicillium notatum* Westling. *A* and *B*, Two-week old colonies of NRRL 821 (type) on Czapek and malt agars. *C*, NRRL 824, The Fleming isolate, on Czapek. *D*, NRRL 1249.B21, a substrain of the Fleming culture that produces unusually high yields of penicillin in surface culture. *E*, NRRL 832, the strain first used for producing penicillin in submerged culture. *F*, NRRL 1950, a strain producing good yields in either surface or submerged culture.

buff or olive-ocher (R., Pl. XXX) to amber or wax yellow (R., Pl. XLI); conidial structures as described above.

Colonies on malt extract agar growing rapidly, 5.5 to 6.0 cm. in 10 to 12 days, plane (fig. 97B), never furrowed, velvety, usually azonate, in clear blue-green shades near sage green to artemisia green (R., Pl. XLVII); exudate lacking; reverse lightly colored in dull orange-brown shades; conidial structures as described above but tending to develop better defined columns of conidia.

Species description centered upon the type strain, NRRL 821, from the Thom Collection as No. 2541, received from Westling in December 1911, as an isolate from branches of *Hyssopus* in Norway; NRRL 824, Fleming's

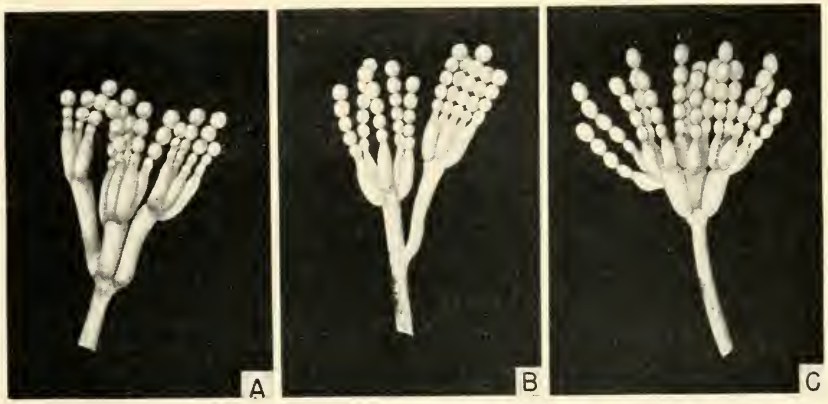


FIG. 98. Penicilli in different strains of *Penicillium notatum*. × 750. *A*, NRRL 824. *B*, NRRL 1950. *C*, NRRL 832. (After Raper and Alexander, 1945 Jour. Elisha Mitchell Scientific Society, *61*, 1945.)

isolation, made at St. Mary's Hospital, London, in 1928, originally reported as *Penicillium rubrum* Biourge, but subsequently diagnosed as *P. notatum* Westling by Thom; NRRL 827, received from Dr. R. St. John Brooks, National Collection Type Cultures, London, in 1936, as a culture from Professor Frederick Challenger, University of Leeds, as a "green mold" capable of volatilizing potassium telluride; NRRL 830 and NRRL 832, from the Biourge collection by Simonart in 1936, in tubes labeled "*obscurum*" and "*lacticus* Maze" respectively; and scores of additional strains isolated and examined over a period of many years. A culture received from the Centraalbureau in February 1946, as *P. griseo-roseum* Dierckx, from Biourge in 1929 and possibly type, duplicates NRRL 827 almost exactly in cultural and microscopical characteristics.

The species is very abundant in nature and shows the same general distribution listed for the series (see p. 374).

Of the above cultures, NRRL 824 (figs. 97C and 98A) is of the greatest interest since it was from this strain that Fleming discovered the antibiotic penicillin (1929), and it was this culture which was employed in all of the early studies on the production and evaluation of this drug. NRRL 832 is likewise of special interest since this strain was the first to be successfully used in the production of penicillin by submerged culture techniques (Moyer and Coghill, 1946b). NRRL 821, Westling's type, produces very low yields of penicillin under all conditions examined.

Penicillium notatum Westling represents a variable species which may appear in a number of fairly distinct cultural forms. When examined apart from a multitude of other forms (which tend to minimize the importance of the criteria that have to be used for separation) some of these might seem to warrant specific or varietal recognition. When, however, large numbers of strains are examined, the significance of such strain variations largely disappears. We believe it prudent to consider all of them within the framework of the single species *P. notatum*. The following strains may be cited as representative of some of the more pronounced cultural types encountered:

NRRL 832 (figs. 97E and 98C), cited above, is marked by restricted but otherwise typical colonies; penicilli usually consist of a single verticil of 3 to 5 metulae and are more compact than most; and conidia range from subglobose to definitely elliptical. The strain is regarded as somewhat transitional toward *Penicillium chrysogenum* Thom. Certain cultural variants (Raper and Alexander, 1945) derived from this strain are of particular interest in that they develop a pronounced vegetative mycelium which is pink to red in color (near daphne red, R., Pl. XXXVIII) and is suspected of being an accentuation of the red or rosy factor reported by Dierckx as characterizing *P. citreo-roseum* and *P. griseo-roseum* (Col. Pl. I).

NRRL 1950 (figs. 97F and 98B), a good penicillin producing strain from which high yielding substrains suitable for surface production were developed (Raper and Alexander, 1945), is marked by comparatively loose-textured colonies with centers often more or less flocculent and marginal areas heavy sporing, velvety, plane or nearly so; abundant yellow exudate and yellow pigmentation in colony reverse are produced; penicilli are regularly small and often consist of two or three terminal metulae bearing small clusters of sterigmata. The pattern of its penicilli is somewhat suggestive of ramigenous members of the Monoverticillata, but cultural and physiological characters unquestionably place it with *P. notatum*.

NRRL 1249.B21 (fig. 97D), a high yielding substrain developed from the original Fleming culture (Raper and Alexander, 1945 and Moyer and Coghill, 1946a), is marked by more rapidly growing colonies that are rather

light sporing, produce little or no exudate upon most substrata, and show colony reverse uncolored or in pale yellow shades. This substrain was employed almost universally for the production of penicillin by the surface culture process (Coghill, 1944).

NRRL 827, cited above, is marked by rapidly growing, comparatively deep, loose-textured, dull blue-green colonies which may develop abundant pale exudate and usually show only a limited yellow pigmentation in reverse. Strains showing this cultural pattern are regularly poor penicillin producers.

Penicillium griseo-roseum Dierckx (Soc. Scien. Brux. **25:** 89. 1901. In Biourge, Monogr., La Cellule **33:** fasc. 1, pp. 168–170; Col. Pl. IV and Pl. VI, fig. 31. 1923; Thom, The Penicillia, pp. 263–264. 1930) as described by Biourge, and as represented by his type strain (reported by Thom in 1930 as No. 4733.70, now maintained as NRRL 820), apparently represents a comparatively deep-growing, loose-textured culture differing little from certain variants known to have developed from well known cultures of *P. notatum* Westling. Biourge reported overgrowths of rosy mycelium in age, a development which is not infrequently seen in some substrains of Fleming's *P. notatum*, and even more strikingly in certain variants of NRRL 832. A culture from the Centraalbureau in February 1946 as *P. griseo-roseum* Dierckx (from Biourge in 1929, and possibly derived from the type also) differs from typical strains of *P. notatum* only in producing deeper, looser-textured colonies with conidial areas in dull blue-green shades and exudate colorless or nearly so. We believe the species should be regarded as synonymous with *P. notatum* Westling. Strains possessing the cultural characteristics of NRRL 820 and the strain from Baarn regularly produce low yields of penicillin.

Penicillium cyaneo-fulvum Biourge, in Monograph, La Cellule **33:** fasc. 1, pp. 174–176; Col. Pl. IV and Pl. VI, fig. 34. 1923; also Thom, The Penicillia, p. 267. 1930.

Colonies on Czapek's solution agar growing fairly rapidly or somewhat restrictedly depending upon the strain, from 2.5 to 4.0 cm. in 10 to 12 days at room temperature, consisting of a loose-textured often more or less floccose felt (fig. 96C) commonly 1 to 2 mm. deep, strongly furrowed in a radial pattern but with central area usually irregularly buckled and wrinkled, with growing margin abrupt, somewhat lobed, white, 1–2 mm. wide, usually light sporing throughout, in light yellow-green shade from gnaphalium green to celandine green, less commonly mineral gray (Ridgway, Pl. XLVII); exudate generally abundant, clear and ranging from almost uncolored in some strains to definitely yellow in others; odor lacking; reverse variable, in dull yellow to yellow-brown shades; conidiophores variable in length, arising from the substratum, or less commonly as branches from aerial hyphae, ranging from comparatively short up to 600 to 800μ or more in length by 2.8 to 3.5μ, with walls smooth and colorless; penicilli bivertcillate and asymmetrical, irregular in pattern, often loosely branched; bear-

ing tangled or loosely parallel chains of conidia up to 50μ in length; branches, when present, about 2.5 to 3.0μ in diameter, extremely variable in length; metulae commonly in verticils of 3 to 4, variable in length from 8 to 15μ, usually 10 to 12μ, with terminal areas commonly enlarged; sterigmata mostly in groups of 3 to 6, comparatively short, 7 to 10μ by 2.0 to 2.5μ; conidia globose to subglobose, mostly 3.0 to 3.8μ in diameter, in some strains larger or smaller, smooth-walled, pale yellow-green in mass.

Colonies on steep agar growing somewhat more rapidly but duplicating the above in general texture and habit, often more closely wrinkled and commonly heavier sporing in somewhat darker shades than above; exudate limited or abundant; odor lacking; reverse in dull yellow to orange-brown shades; penicilli more abundantly produced but similar to the above in pattern and dimensions.

Colonies on malt extract agar, from 4 to 6 cm. in diameter in 2 weeks, plane, ranging from strictly velvety to more or less floccose (fig. 96D) depending upon the strain, comparatively heavy sporing in dull glaucous blue to gray-green shades (R., Pl. XLII); exudate lacking; reverse in dull orange-brown shades; details of penicilli as on Czapek but with conidial chains commonly longer.

Species description centered upon NRRL 837, from the Thom Collection as No. 4733.47, representing Biourge's type received in 1924. Represented also by NRRL 839, from Simonart as Biourge's strain, possibly duplicating the above in origin but now showing minor cultural differences. This latter strain is duplicated by a culture received from the Centraalbureau in February 1946, under the same name and probably stemming from the same source.

Cultures of the kind described above regularly produce low yields of penicillin.

The validity of this species is somewhat in doubt because in studies of variation within the series mutants of *Penicillium notatum* have been observed which approximate this species. However, since the general type of culture described here has been obtained from widely separated natural sources, and since Biourge's strains have in general retained their character for twenty years or more in culture, it seems best to recognize such a species as *P. cyaneo-fulvum*. In cultural characteristics, strains in our collection as type material of *P. citreo-roseum* Dierckx, *P. griseo-roseum* Dierckx, and *P. chlorophaeum* Biourge (see p. 363) bear a striking resemblance to *P. cyaneo-fulvum* Biourge. Admittedly, the selection of *P. cyaneo-fulvum* for recognition is somewhat arbitrary.

Penicillium brunneo-rubrum Dierckx (Soc. Scien. Brux. **25:** 88. 1901; in Biourge, Monogr., La Cellule **33:** fasc. 1, pp. 176–179; Col. Pl. IV and Pl. VI, fig. 36. 1923; Thom, The Penicillia, pp. 267–268. 1930) as reported by Biourge and as known from

his type strain, discussed by Thom in 1930 as No. 4733.22 and now maintained as NRRL 841, represents a comparatively deep, rather flocculent, medium sporing member of the *P. chrysogenum* series which is regarded as approximating *P. cyaneo-fulvum* Biourge. Conidia are comparatively large and somewhat elliptical, and colonies on Czapek's agar produce abundant yellow exudate and bright yellow pigments in reverse. A culture received from the Centraalbureau in February 1946 as *P. brunneo-rubrum* Dierckx from Biourge in 1929, and probably from the same original source as NRRL 841, differs from it in producing heavier sporing colonies that are light blue-green in color with limited clear exudate and reverse almost colorless. In this, as in many other cultures long maintained in laboratory culture, there is evidence of marked variation.

Penicillium citreo-roseum Dierckx (Soc. Scien. Brux. **25**: 86. 1901; in Biourge, Mongr., La Cellule **33**: fasc. 1, pp. 182–184; Col. Pl. IV and Pl. VII, fig. 38. 1923; Thom, The Penicillia, pp. 265–266. 1930) as known from Biourge's description and his type strain, reported by Thom in 1930 as No. 4733.36 and now maintained as NRRL 834, is regarded as approximating *P. cyaneo-fulvum* Biourge. Cultures are comparatively deep, medium sporing, light blue-green in color, produce abundant light straw colored to pale amber exudate, and colony reverse in yellow to golden yellow shades. A strain received from the Centraalbureau in February 1946 as a culture of *P. citreo-roseum* Dierckx from Biourge (in 1937) essentially duplicates NRRL 834 except for reduced exudate formation. Biourge's concept of Dierckx's species appears to have been based upon a strain which developed reddish colors in the colony surface and reverse, and Thom in 1930 noted the reverse as "yellow then slowly red in center." Neither the strain maintained at this Laboratory nor that from Baarn now exhibit this distinguishing characteristic. There appears to be no other basis for separating it from other more or less flocculent, light to medium sporing strains that are pale blue-green or gray in color and produce globose to subglobose conidia. These are regarded as representing or approximating *P. cyaneo-fulvum* Biourge.

Occurrence and Significance

Members of the *Penicillium chrysogenum* series regularly occur in soil and are commonly found upon a wide variety of organic substrata, including: cheese and other dairy products, bread and pastries, fruits, vegetables, meat and meat products, improperly canned foods, and decaying vegetation of all kinds (Raper, Alexander, and Coghill, 1944). Representative cultures have come from every region from which either cultures or materials have been examined. The species assigned here are unquestionably world-wide in distribution.

Principal interest in this series stems from the capacity of these molds to produce the antibiotic penicillin. Since so much work has been done on this fermentation during the past few years, and since so many papers have been published, we have included a separate chapter covering the history, significant developments, and present status of this fermentation (see Chapter V).

Since molds belonging to the *Penicillium chrysogenum* series are unusually abundant in nature it is neither surprising that they are commonly asso-

ciated with processes of spoilage or deterioration, nor that they are often used as test species in microbiological investigations. Bisby, *et al.* (1933) reported *P. chrysogenum* and *P. terrestre* to be common in butter and recommended the addition of an increased amount of salt as a protective measure. Groom and Panisset (1933) found *P. chrysogenum* to be the most prevalent mold associated with "mildew" of book materials in the Public Records Office in London. Swift (1931) reported *P. meleagrinum* to grow in the fine cracks developing in painted pottery, producing an effect commonly referred to as "crazed crockery." Semeniuk and Ball (1937) reported *P. chrysogenum* and *P. notatum* to be common on meats in cold storage lockers in Iowa. Panassenko and Tatarenko (1940) reported *P. chrysogenum* and *P. puberulum* to be able to grow at unusually low temperatures, hence to commonly occur upon meat and other foodstuffs in cold storage. Nagel and Semeniuk (1947), investigating the molding of shelled corn, found *P. chrysogenum*, *Aspergillus niger*, and *A. flavus* to be the most active decomposers of maize organic matter.

Everitt and Sullivan (1940) studied the fungistatic and fungicidal action of fifty organic sulphur compounds against Fleming's strain of *Penicillium notatum* and several common molds. Mercaptobenzothiazole was the most active compound tested, inhibiting the growth of all test strains at 50 to 100 p.p.m. Kampf and Nungester (1944) reported sodium azide in high dilutions to inhibit the growth of *P. notatum*, *A. niger*, and other molds. Gonzalez (1945) investigated the inhibitory effect of vitamin K and two other quinones upon *P. notatum*. Ramon and Richou (1945) found *P. notatum* able to grow in concentrations of formaldehyde sufficient to inhibit most bacteria. Gustafson (1920) had earlier investigated the effect of H-ion concentration on the respiration of *P. chrysogenum*.

Members of the *Penicillium chrysogenum* series are fairly active biochemically and produce a number of interesting metabolic products in addition to penicillin. Birkinshaw and Raistrick (1931) reported *P. chrysogenum* to produce some gluconic acid and mannitol. May, *et al.* (1934) found a selected strain of the same species (Thom's No. 5034.11 = NRRL 811) to produce good yields of gluconic acid from glucose. When grown submerged under three atmospheres air pressure, and with added $CaCO_3$, further improvements were realized and yields of 80–87 per cent (based on the sugar consumed) were obtained in 8 days. In a separate paper, Moyer, *et al.* (1936) discussed the nutrition of this mold and the influence of the surface area to volume ratio in relation to gluconic acid production in surface cultures. The addition of $FeCl_3$ stimulated vegetative growth and increased acid production when high-purity nutrients were used. Lenti (1940) discussed the various steps in carbohydrate metabolism by a strain of *P. chrysogenum*. More recently Wolf (1947) has carefully investigated

the oxidation of various sugars and other carbohydrates by the Fleming strain of *P. notatum* (NRRL 1249).

Phaff (1947) used a strain of *Penicillium chrysogenum*, grown upon a synthetic medium, as a source of exocellular pectic enzymes. The formation and adaptive nature of polygalacturonase and pectinesterase were discussed.

Manceau, *et al.* (1938) reported the production of a reducing substance resembling but not duplicating ascorbic acid by two Penicillia reported as *Penicillium citreo-roseum* Dierckx and *P. ochraceum* Bainier. Tanner, *et al.* (1945) investigated the vitamin and protein content of residues from penicillin fermentations involving strains of *P. notatum* and *P. chrysogenum*. Pantothentic acid was increased ten-fold over that in the basal medium, whereas pyridoxin potency was doubled. Other B vitamins, including niacin, riboflavin, and biotin were only slightly increased. The protein content of the penicillin residues (including the mycelium), was slightly higher than that of the unfermented medium.

Cavallito (1944) reported the mycelium of *Penicillium notatum*, *P. chrysogenum*, and *P. citrinum* to consistently contain about 1.1 per cent ergosterol when the molds were grown in surface cultures. Submerged fermentations were unfavorable for its production. Zook, *et al.* (1944) isolated ergosterol in 1 per cent yield from the dried mycelium of *P. notatum* grown for the production of penicillin. Whether the cultures were surface or submerged was not disclosed. Savard and Grant (1946) isolated ergosterol in low yields from the mycelium of strain X-1612 (incorrectly cited as *P. notatum* rather than *P. chrysogenum*) grown commercially in submerged culture for penicillin production. Nilsson, *et al.* (1945) compared the ergosterol content of dried powdered *P. notatum* mycelium, *Torula utilis*, and Brewer's yeast and reported these to contain 0.85 per cent, 0.26 per cent, and 0.31 per cent respectively. Upon irradiation the ergosterol of *P. notatum* yielded vitamin D_2.

Several investigators have isolated and studied pigments produced by members of the *Penicillium chrysogenum* series. Clutterbuck and Lovell (1931) and Clutterbuck, Lovell, and Raistrick (1932) reported the production from glucose of a light yellow, strongly laevorotatory pigment, for which they provisionally gave the empirical formula $C_{18}H_{22}O_6$ and which they designated chrysogenin. Methods for production, isolation, and characterization of the pigment were given. In the same papers they discussed the synthesis of an alkali soluble protein from glucose as the sole source of carbon and $NaNO_3$ as the sole source of nitrogen. Penicillin was likewise produced on the synthetic medium by Fleming's strain of *P. notatum*, and limited attention was given to its properties. Stodola, *et al.* (1945) described the production by *P. notatum* of a new pigment, peni-

trinic acid. The pigment is an optically active, yellow, crystalline carboxylic acid, melting with decomposition at 217 to 223°C., and having the composition $C_{15}H_{17}O_5N$. By decarboxylation in acid and alkaline solutions, penitrinic acid gave isomeric products of the composition $C_{14}H_{17}O_3N$, designated as α-penitrin and β-penitrin, respectively. These appeared to be phenols. Posternak and Jacob (1940) described the production of an orange-yellow pigment from *P. citreo-roseum* Dierckx, designated citreoroseine and having the empirical formula $C_{15}H_{10}O_6$. The pigment appeared to be an anthraquinone. Kuhn (1943) reported *P. notatum*, *P. chrysogenum*, and *P. meleagrinum* in the presence of H_3BO_3 to form a luminous, yellow, greenly fluorescent, pigment, designated borocitrine. The same species were the only three out of 24 species of Penicillia tested which produced penicillin. Tauber and Laufer (1943) studied the color reactions of several natural pigments, including that of *P. chrysogenum*.

In addition to penicillin, *Penicillium notatum* produces another substance with marked antibiotic properties, variously designated as penatin (Kocholaty, 1942a, 1942b, 1943a, and 1943b), notatin (Coulthard, *et al.*, 1942; Birkinshaw and Raistrick, 1943; and Coulthard, *et al.*, 1945), and penicillin B (Roberts, *et al.*, 1943). This antibiotic is a protein and acts as a glucose oxidase, exerting its powerful antibiotic action by the liberation of H_2O_2. It is highly toxic to animals and man. Since it occurs under conditions that are not conducive to the formation of penicillin, it does not, however, interfere with the production of the more useful antibiotic. Coulthard, *et al.* (1945) isolated in crude form an antibacterial substance from *P. resticulosum* (see p. 457) which they regarded as probably identical with notatin.

Penicillium oxalicum Series

Outstanding Characters

Colonies broadly spreading, velvety, plane or developing irregular or radial furrows, heavily sporing throughout, in dull to dark blue-green shades, with conidia often forming deep layers which break off when the culture dish or tube is tapped, releasing a cloud of spores.

Conidiophores typically arising from the substratum in a dense stand, variable in length but usually less than 200μ, smooth-walled.

Penicilli biverticillate, asymmetrical, consisting of 2 or more metulae bearing sterigmata, or irregularly branched, with branches and metulae sometimes arising at the same level, often closely appressed.

Sterigmata closely parallel, commonly bearing conidia in adherent chains producing loose to compact spore columns up to 500μ or more in length.

Conidia consistently elliptical, smooth-walled.

Series Key

b. Colonies not producing yellow pigment in exudate or colony reverse; conidia commonly 5.0μ or more in long axis, strongly elliptical.
1′. Conidia elliptical, fairly uniform in size; common in soil. . . . *P. oxalicum* series
aa. Colonies plane or nearly so, conidia often forming deep crusts, conidial chains appearing "silky" when viewed under low power.
P. oxalicum Currie and Thom
bb. Colonies radially furrowed, not forming crusts, reverse in maroon shades.
P. atramentosum Thom

The series is recognized as probably artificial in character and is introduced largely as a matter of convenience to include two well-marked, velvety species with elliptical, smooth-walled conidia.

One of these species, *Penicillium oxalicum* Currie and Thom is especially common in soil and upon various organic materials undergoing slow deterioration or decay. It is world-wide in distribution and is undoubtedly one of the most ubiquitous of all the Penicillia. The species has long been known to represent a normal component of the mycoflora of soils generally, and it has been repeatedly encountered among the cultures isolated from tentage and other military equipment subjected to field conditions. As the name implies, typical strains produce some oxalic acid, although the amount produced is generally much less than that from selected cultures of *Aspergillus niger*. The species is marked particularly by its very abundant spore production in newly isolated strains. In their typical aspect, these are uniformly and deeply velvety and not infrequently develop continuous layers of spores from 0.5 to 1.0 mm. deep over the entire colony area (figs. 100A and B). Viewed with a hand lens, the colony surface commonly has a silky appearance. When the culture dish or tube is lightly tapped the conidia are loosened and break away as shown in figs. 100C and D; or when sharply struck they produce a dense cloud quickly filling the culture vessel. The species is further distinguished by its large, strongly elliptical, smooth-walled conidia. These originate as cylindrical cells hardly distinguishable from the terminal areas of the parent sterigmata, but as they mature they gradually assume their characteristic elliptical form.

The second species, *Penicillium atramentosum* Thom is doubtfully closely related to *P. oxalicum*. Yet the two species possess sufficient characters in common to enable the mycologist to locate the species here more readily than anywhere else. Colonies of *P. atramentosum* on Czapek are usually azonate, radially furrowed and strictly velvety (fig. 101A); penicilli are usually biverticillate and asymmetrical, smooth-walled throughout, and bear smooth-walled elliptical conidia. Unlike *P. oxalicum*, which is unusually common and widely distributed, *P. atramentosum* appears to be comparatively rare. Of three numbered strains available for the present study, two are known to have stemmed from the type culture which was

isolated by Thom more than forty years ago. Some additional strains have been examined in the intervening years, but the number has been limited. Although the type was isolated from cheese, it is probably safe to regard the species as typically a soil fungus.

Penicillium oxalicum Currie and Thom, in Jour. Biol. Chem. **22:** 289, fig. 1. 1915; also Thom, The Penicillia, pp. 247–248, fig. 31. 1930

Colonies upon Czapek's solution agar broadly spreading, attaining a diameter of 3.5 to 5.0 cm. in about 10 days at room temperature, generally plane (fig. 100A) but in some strains irregularly furrowed (fig. 100F), strictly velvety in typical strains including most new isolates, heavily sporing with conidia forming a deep layer which, when mature, characteristically falls away *en masse* if the culture vessel is tapped (fig. 100C and D), shading from pale blue-green in young spore areas to dull green shades near sage green (Ridgway, Pl. XLVII) or blue-green shades near Russian green (R., Pl. XLII) in colony centers, becoming slate olive to deep slate-olive (R., Pl. XLVII) or storm to castor gray (R., Pl. LII) in age, vegetative mycelium largely submerged, often extending 2 mm. or more beyond the limits of conidium production, growing marginal zone 1 to 2 mm. wide, white or nearly so, becoming blue-green with the development of conidia; generally producing no exudate; no odor; colony reverse uncolored in some strains but generally in yellowish, orange, or more commonly pink shades; penicilli typically biverticillate and asymmetric (fig. 99A), produced in great abundance, borne upon smooth-walled conidiophores 100 to 200μ by 3.5 to 4.5μ arising from the substratum in a close stand to produce a velvety colony surface, occasionally monoverticillate but normally biverticillate with 2 or 3 metulae, or metulae and branches arising from the same level, with all cellular elements appressed and with conidial chains forming columns up to 500μ or more in length by 10 to 15μ in diameter, appearing silky when viewed under very low magnifications, becoming entangled with similar columns from adjacent penicilli to form a deep spore layer which breaks off in the manner noted above; branches absent or borne singly, 10 to 20μ by 3.5 to 4.5μ, often arising from the same level as one or more metulae; metulae usually in groups of 2 or 3, rarely more, 15 to 20μ by 3.3 to 3.8μ; sterigmata borne in terminal clusters of 6 to 10, rarely more, 9.0 to 15.0μ by 3.0 to 3.5μ, with conidium-bearing tips more or less tapered; conidia persistently elliptical (fig. 99A_2), smooth-walled, ranging from 4.5 to 6.5μ by 3.0 to 4.0μ, but mostly 5.0 to 5.5μ by 3.0 to 3.5μ.

Colonies upon steep agar, and to a less extent upon malt agar, grow more rapidly (fig. 100B), tend to be less deeply furrowed, and are generally heavier sporing than upon Czapek agar, producing heavy layers of conidia

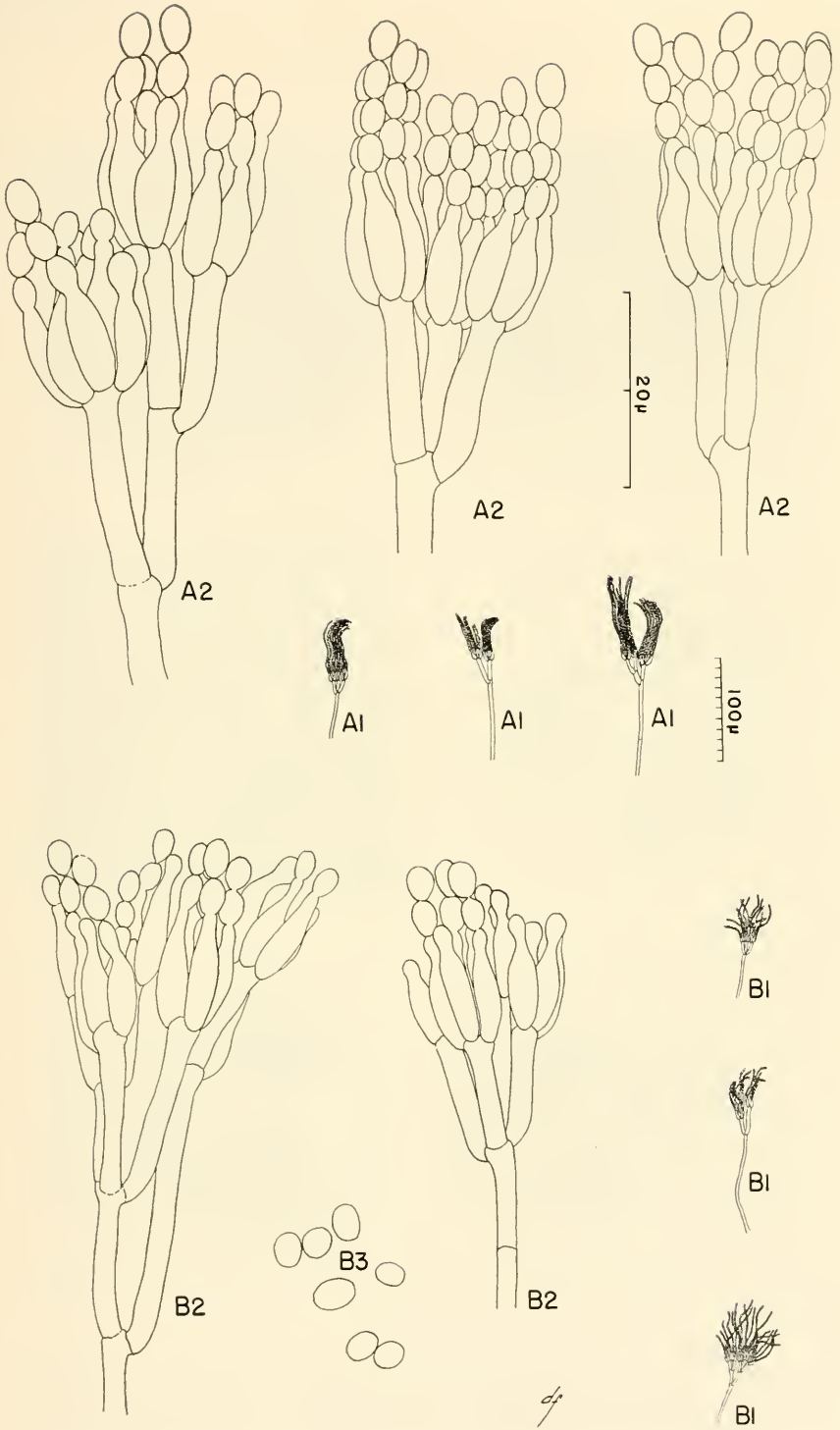


FIG. 99. *Penicillium oxalicum* series. *A*, *P. oxalicum* Currie and Thom: A_1 and A_2, Habit sketches and detailed drawings of representative penicilli, respectively. *B*, *P. atramentosum* Thom: B_1 and B_2, Habit sketches and detailed drawings of typical penicilli, respectively; B_3, conidia.

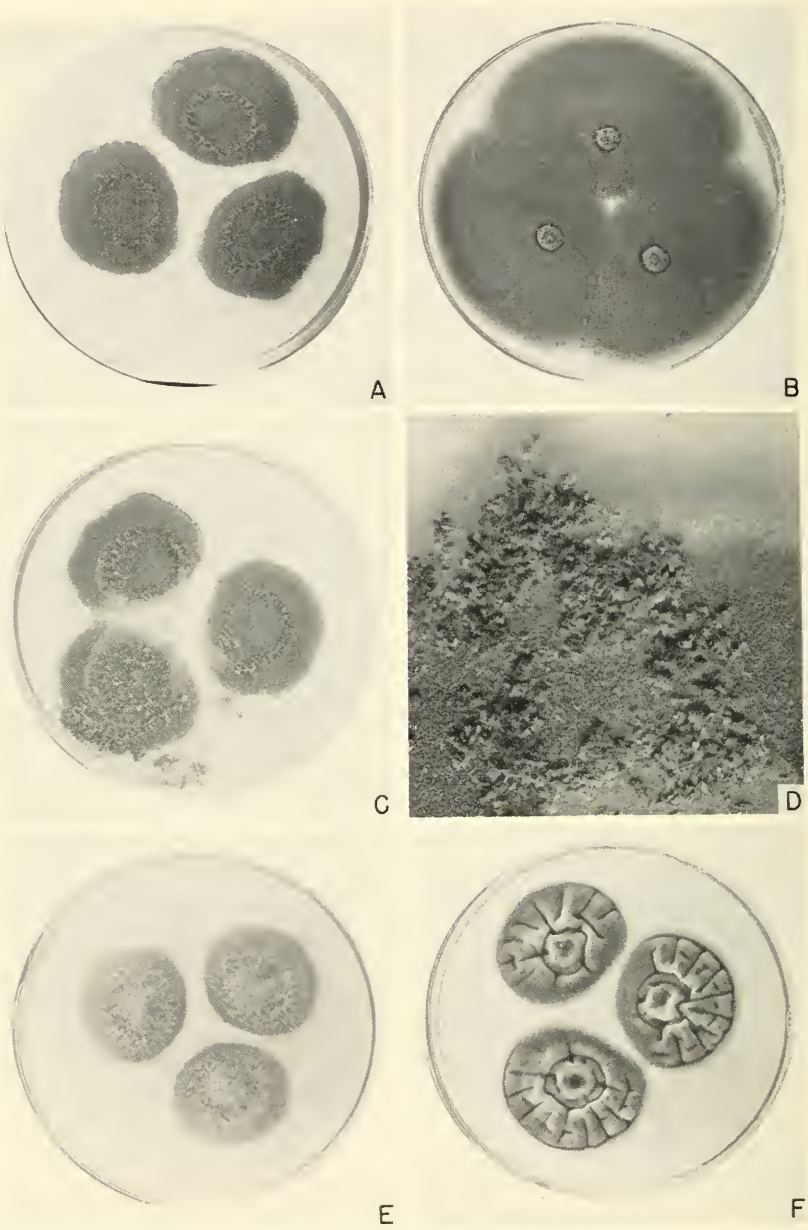


FIG. 100. *Penicillium oxalicum* Currie and Thom. *A* and *B*, Ten-day old colonies of a typical, heavy-sporing strain, NRRL 2139, growing on Czapek and steep agars. *C*, Same culture as shown in *A*, but after petri dish has been jarred, breaking the heavy crusts of conidia that characterize this species. *D*, Slightly enlarged area showing dislodged masses of conidia, × 6. *E*, NRRL 787 (type strain—see text) on Czapek. *F*, NRRL 790, on Czapek, characterized by strongly wrinkled colonies.

which break off readily as crusts when mature; penicilli are essentially like those produced upon Czapek.

Strains of *Penicillium oxalicum* commonly show progressive variation under continued laboratory cultivation, and in time produce colonies that are loose textured, light sporing and more or less floccose or even funiculose (fig. 100E), and which usually exhibit a flesh to light pink coloration, at least in more strictly mycelial areas. Fruiting structures, although relatively few in number, generally remain essentially typical in pattern with the form and dimensions of conidia and spore bearing parts unchanged.

Species diagnosis is based upon typical cultures contained in the NRRL Collection such as NRRL 790, received in 1934 from S. A. Hall as a strain of "Danish Roquefort" mold; NRRL 1836, isolated in 1942 from South Carolina soil; NRRL 2139, isolated from moldy leather and received in September 1944 from T. C. Cordon, Eastern Regional Research Laboratory, Wyndmoor, Pennsylvania; and innumerable other strains isolated from soils and various organic substrates undergoing slow aerobic decomposition.

Currie and Thom's description was based upon Thom's culture No. 103 (NRRL 787) as type. In 1915 this strain produced velvety, heavily sporing colonies conforming with the species description as given above, but during the more than 30-year period that it has been maintained in laboratory culture it has exhibited a gradual and progressive variation away from the original (fig. 100E) until today it could hardly be assigned to this species except for the fact that it has been under continual observation and that its conidial structures, although sparsely produced, still conform in general to those of more typical strains. Other cultures when maintained in the laboratory over considerable periods show similar variation and we are led to believe that the tendency of strains to become more floccose and less heavily sporing represents a true species character.

Penicillium oxalicum is cosmopolitan in its habitats and apparently world-wide in distribution. It is especially common in soil and upon plant residues undergoing slow decomposition.

Penicillium atramentosum Thom, in U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, pp. 65–66, fig. 24. 1910. Emended in Thom, The Penicillia, pp. 251–252. 1930

Colonies upon Czapek's solution agar spreading, attaining a diameter of 5.0 to 6.0 cm. in 10 days at room temperature, comparatively thin, heavily sporing, velvety except for the presence of limited sterile hyphae in central colony areas, strongly furrowed in a predominantly radial pattern but with less regularity in central than in submarginal zones (fig. 101A), marginal area 2.0 to 3.0 mm. wide, thin, white to pale blue-green with the develop-

ment of young spore-bearing structures, fruiting areas light bluish green at first but soon becoming sage green (Ridgway, Pl. XLVII) to Russian green (R., Pl. XLII) and eventually dark olive in age, usually azonate but at times broadly and indistinctly zonate; reverse in deep orange-red to mahogany shades in colony centers, shading through lighter tints of the same shades toward the margin; odor slight, not distinctive; conidial structures abundant, arising primarily from the substratum, less commonly from surface hyphae, usually appearing as a close and regular stand of erect fructifications; penicilli asymmetrical, 25 to 40μ in length, showing considerable irregularity in size and pattern (fig. 99B$_2$), in most cases consisting of a terminal verticil of 2 to 4, more or less, divergent metulae, in others branched with one or more metulae borne upon each branch in addition to the terminal stem, in scattered instances appearing monoverticillate,

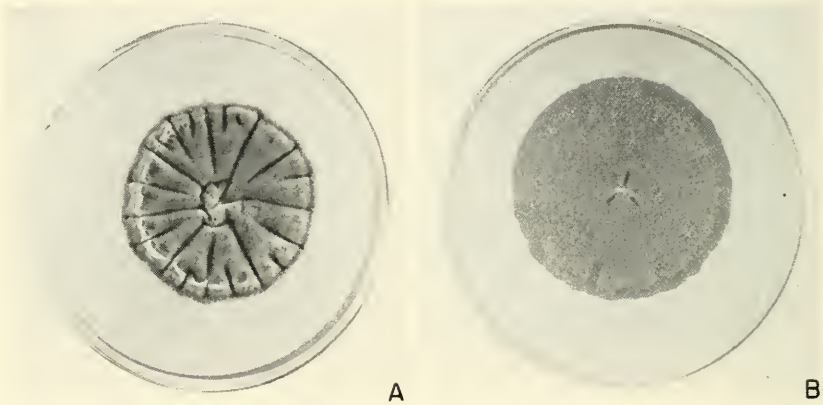


FIG. 101. *Penicillium atramentosum* Thom, NRRL 795. *A* and *B*, Two-week old colonies on Czapek and malt agars.

chains of conidia adhering into poorly defined columns (fig. 99B$_1$), or more divergent and becoming tangled with those of adjacent heads, commonly 50 to 75μ in length, rarely more than 100μ; conidiophores very irregular in length, commonly 50 to 75μ but ranging from 25 to 125μ, mostly 2.5 to 3.5μ in diameter, with all walls smooth; branches when present 8.0 to 15.0μ by 2.5 to 3.0μ; metulae 8.0 to 13.0μ by 2.2 to 2.8μ; sterigmata in verticils of 2 to 6, somewhat variable in form, mostly 8.0 to 12.0μ by 2.0 to 2.8μ; conidia mostly elliptical, less commonly subglobose 3.0 to 4.0μ by 2.8 to 3.5μ, smooth-walled (fig. 99B$_3$).

Colonies on steep agar growing somewhat more rapidly than on Czapek, more closely and conspicuously furrowed but like the above in texture and general coloration, and producing similar penicilli.

Colonies upon malt extract agar 5.0 to 6.0 cm. in diameter in 10 days at room temperature, plane, velvety, azonate, heavily sporulating (fig. 101B),

uniformly sage green (R., Pl. XLVII) to Russian green (R., Pl. XLII), with reverse at first uncolored becoming darker in age, characterized by a distinct and often pronounced odor of black walnuts; penicilli as described above.

The species description is based primarily upon NRRL 795. This strain was isolated by Thom from cheese at Storrs, Connecticut in 1905, and furnished the type material for the species description as published by him in 1910. The strain was designated No. 38, and as such, was sent to various European laboratories. It was subsequently lost by Thom, but was later returned to him by Biourge as the latter's No. 161 and was reentered in the Thom Collection as No. 4733.3. Biourge discussed the species and strain in his Monograph (La Cellule **33:** fasc. 1, pp. 260–262, Col. Pl. IX, Pl. XIV, fig. 84. 1923) as it appeared on wort gelatine. Biourge's cultural data is presented together with a condensation of Thom's original description based upon potato and bean agars in Thom's Monograph (The Penicillia, p. 252. 1930), and a very brief statement regarding the appearance of the culture on Czapek's solution agar. The culture has remained remarkably stable during more than forty years that it has been under laboratory cultivation.

Two additional entries assigned to this species are contained in our Collection: One of these, NRRL 796, was received from Biourge as *Penicillium frequentans* Westling (Thom's No. 4733.63) but proved to belong here. The second, NRRL 797, was brought to this country in 1936 by Dr. Paul Simonart from Biourge's laboratory as the latter's No. 161, *P. atramentosum* Thom, and thus stems from the same culture as NRRL 795.

The species does not appear to be widely distributed in nature but possesses sufficient distinctive characteristics in its cultural habits, and to a lesser degree in its structural detail, to warrant its continued recognition. Representatives of the species are occasionally isolated from soil.

While this species is not regarded as closely related to *Penicillium oxalicum* Currie and Thom, we believe that it will be located here more readily than elsewhere because of its velvety habit, its comparatively simple asymmetric penicilli and its elliptical smooth-walled spores. It differs markedly from *P. oxalicum* in its failure to develop heavy crusts of conidia and in the development of comparatively deep red to mahogany colors in reverse. The production of a pronounced odor of black walnuts on malt agar is suggestive of certain members of the Biverticillata-Symmetrica, particularly *P. purpurogenum* Stoll. Whatever similarity exists probably represents a coincidence rather than an indication of close relationship.

Occurrence and Significance

The common occurrence and wide distribution of *Penicillium oxalicum* in soil is presumed to indicate an active role in aerobic processes of decomposition. However, specific reports substantiating such activity are lack-

ing. Harrison (1934) noted its presence in hay undergoing thermogenic spoilage although the optimum temperature of the species was listed as 25°C. Peele and Beale (1940) reported *P. oxalicum* and *Fusarium moniliforme* to promote aggregation and granulation in Cecil clay loam soil. The inoculation of non-sterile soil containing sucrose or ground oat straw resulted in greater aggregation than in uninoculated controls. Similar treatments in field plots increased granulation and decreased run-off and erosion.

Penicillium oxalicum usually exists in nature as a true saprophyte. Nevertheless, it is capable of becoming parasitic under certain conditions. As shown by Johann (1928 and 1929), Koehler and Holbert (1930), and Johann, Holbert, and Dickson (1931), it sometimes causes serious infections of corn seedlings, being especially destructive of certain inbred strains. Johann, *et al.* (1931) observed that the fungus damaged or killed the seedlings indirectly rather than by direct invasion of healthy cells, and suggested that sufficient oxalic acid might be produced to kill cells in advance of the fungus. The fungus commonly develops on the ear at the base of the kernels in immature or improperly dried seed corn, hence furnishes a ready source of infection when planted.

Diachun (1939) found *Penicillium notatum* and *Penicillium* sp., isolated from a corn ear in the field, to afford partial protection against infection by *P. oxalicum*, but no antagonism between the strains was observed in culture. A substance toxic to corn seedlings was produced by *P. oxalicum* when grown on Richard's solution and on autoclaved or living corn kernels. Ho (1944) reported *P. oxalicum* as a moderately destructive soil fungus attacking the roots of maize. Leukel and Martin (1943) reported *P. oxalicum* as one of the more important fungi producing seedling blight in sorghum. It was likewise highly destructive of kernels which sustained seed coat injuries during threshing.

Kirsh (1935a) obtained from *Penicillium oxalicum* and *Aspergillus flavus* a water soluble enzyme, or lipase, capable of hydrolyzing olive oil. Maximum production was realized on a bran-soybean medium at 28°C. at the time of greatest sporulation. A preparation was secured which contained 8.5 times more lipase per unit of protease than did a commercial "high-lipase trypsin". Investigating the properties of the lipase further, Kirsh (1935b) found its optimum pH to be 5.0 and its optimum temperature 37–40°C. Activity was rapidly lost upon storage, and complete inactivation occurred in one hour at 60°C. The lipase was non-specific, hydrolyzing corn, cottonseed, cod liver, and sesame oils to the same extent as olive oil.

Currie and Thom (1915) described *Penicillium oxalicum* as producing oxalic acid in excess of other organisms tried. When calcium carbonate was added to the media the mold grew poorly but the yield of acid was

greatly increased, reaching at times 40 per cent of the sugar employed. Oxalic acid so produced was not an end product but reached a maximum in eight to twelve days and then diminished. *Penicillium oxalicum* produced acid from sucrose, lactose, and potato starch.

Sinha (1946) reported *Penicillium atramentosum* to be one of several molds causing a decay of mangoes in the United Provinces.

Penicillium digitatum Series

("Green Rot" of Citrus Fruits)

Outstanding Characters

Colonies on Czapek solution agar growing very thinly and very restrictedly, characterized by a limited submerged vegetative mycelium bearing comparatively few and very irregular, asymmetric penicilli.

Colonies on steep and malt agars growing luxuriantly, spreading broadly, loose-textured, velvety or nearly so, fairly heavy sporing in dull yellow-green shades, becoming grayish olive in age; odor pronounced, strongly aromatic, variously described as suggesting decaying citrus fruits or unfermented dill pickles.

Conidiophores coarse, comparatively short, arising from submerged hyphae or from the basal mycelial felt, smooth-walled.

Penicilli asymmetric, very irregular in size and pattern, with identity of branches and metulae often poorly established, bearing sterigmata and conidial chains at various levels in the penicillus. Cellular elements usually large, coarse, and irregular.

Conidia at first cylindrical, usually becoming elliptical or occasionally subglobose, extremely variable in size but larger than in almost any other series.

Typically produces an olive green rot of citrus fruits. Rarely observed upon or isolated from other substrata.

The series is represented by a single species, *Penicillium digitatum* Sacc., which is responsible for serious losses of citrus fruits in commerce. In its natural habitats (figs. 103A and B), this mold produces an olive-colored rot characterized by the presence of a dense, powdery layer of olive-colored conidia. Growth on citrus fruits is very rapid, and starting from small localized infections, the molds can completely cover the surface of an orange, lemon, or even a large grapefruit within 3 to 4 days at 20 to 24°C. Such fruits, when exposed to the air, dry up rapidly, shrink in size, and eventually become hollow, mummified shells, dull olive-brown in color. Members of the *P. italicum* series (pp. 523–531), on the other hand, as they infect citrus fruits, produce blue-green conidial masses in greater or less abundance and

cause a soft rot from which the fruit quickly loses its shape and may become a flattened slimy mass. Observed upon fruit, the two series can generally be easily distinguished; once isolated and grown in plate cultures, the two are unmistakable. Members of the two series occasionally occur in mixed infections although one or the other usually predominates sufficiently to determine and characterize the type of resulting decay.

Cultivated in the laboratory, members of the *Penicillium digitatum* series are characterized by their sparse growth and limited spore production upon Czapek's solution agar and other comparable synthetic media based upon comparatively pure sugars and inorganic nitrogen sources. They are equally characterized by their luxuriant growth and abundant sporulation upon malt extract and potato-dextrose agars, and upon Czapek's solution agar to which amendments such as steep liquor or yeast extract have been added. Upon enriched media of the latter type colonies spread rapidly, and are essentially plane and velvety. As abundant conidial structures develop, they assume a dull yellow-green to light olive color. Penicilli are typically biverticillate and asymmetric but vary greatly in size and pattern, and in being mounted show a pronounced tendency to break up into the many cellular elements of which they are composed. The preparation of satisfactory mounts is difficult even from very young cultures due to the deciduous character of sterigmata and metulae.

While a number of species belonging to this general series have been described by Sopp (1912), Wehmer (1895), and others, the writers do not believe that any of these differ from Saccardo's material and description sufficiently to warrant continued retention as separate species.

Penicillium digitatum Saccardo, in Mycotheca Italica as No. 986, Herbarium U. S. Dept. Agr.; in Sylloge Fungorum, Vol. IV: 78, 1886; in Fungi Italici, No. 894. Also Thom, U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, pp. 31–33, fig. 3. 1910; and The Penicillia, pp. 242–245, figs. 29 and 30. 1930

Colonies upon Czapek's solution agar growing restrictedly, attaining a diameter of about 1 cm. in 10 to 14 days at room temperature (fig. 103C), growth very thin, with vegetative mycelium largely submerged and bearing few conidial structures of small dimensions and of irregular pattern, usually consisting of a limited number of sterigmata bearing conidial chains up to 150μ in length, variously supported by branches and/or metulae of variable dimensions (for description of penicilli, see malt agar below). Withal, colonies present the general aspect of a mold suffering from some type of nutritional deficiency.

Colonies upon steep agar growing luxuriantly (fig. 103D), spreading, attaining a diameter of 6 to 8 cm. in 10 to 14 days at 24°C., rather loose-

textured but essentially velvety, plane, consisting of a well-developed vegetative mycelium at the agar surface upon which are borne abundant conidial structures, margins essentially white, 2 to 4 mm. wide, and more or less fimbriate in rapidly growing colonies, sporulating areas in dull yellow-green shades near tea green and vetiver green (Ridgway, Pl. XLVII) when young, becoming grayish olive (R., Pl. XLVI) in age; no exudate produced; odor pronounced, strongly aromatic, suggestive of decaying citrus fruits or dill as used in pickle manufacture; reverse uncolored or showing light to dull brown shades.

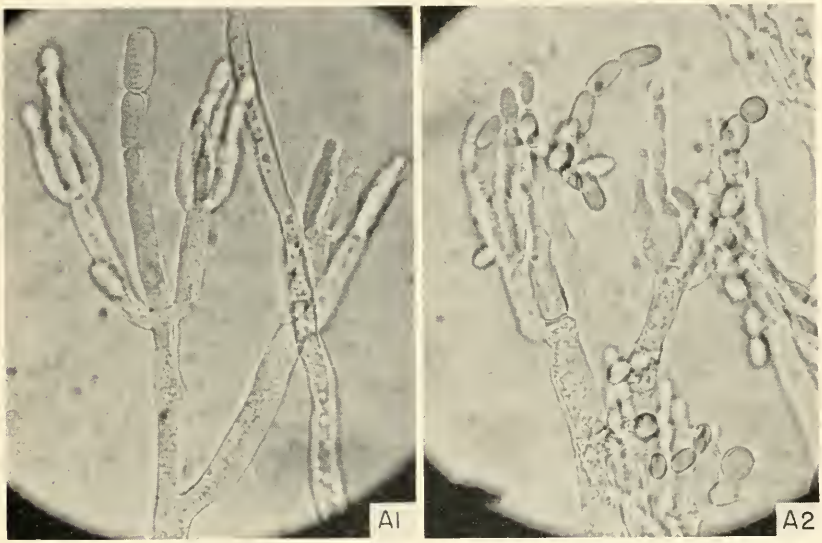


FIG. 102. *Penicillium digitatum* Saccardo. A_1 and A_2, Details of penicilli showing their characteristic irregular pattern, and cylindrical to strongly elliptical conidia which are unusually variable in size, × 750.

Colonies upon malt extract agar growing rapidly, attaining a diameter of 6 to 8 cm. in 10 to 14 days at 24°C., plane, velvety, closer-textured and slightly heavier sporing than upon steep agar, but in general showing the same cultural characteristics and coloration as upon that substrate; odor pronounced, aromatic as on steep agar; reverse uncolored or in dull tan shades; vegetative hyphae coarse, but consistently thin walled, varying in diameter from 4.0 to 5.0μ as a rule, but up to 8.0 to 10.0μ in occasional instances; conidial structures characterized by great irregularity in the number and dimensions of parts (fig. 102), but usually consisting of an indefinite number of branches and/or metulae supporting a limited but variable series of spore-bearing cells or sterigmata, each terminating in a chain of conidia

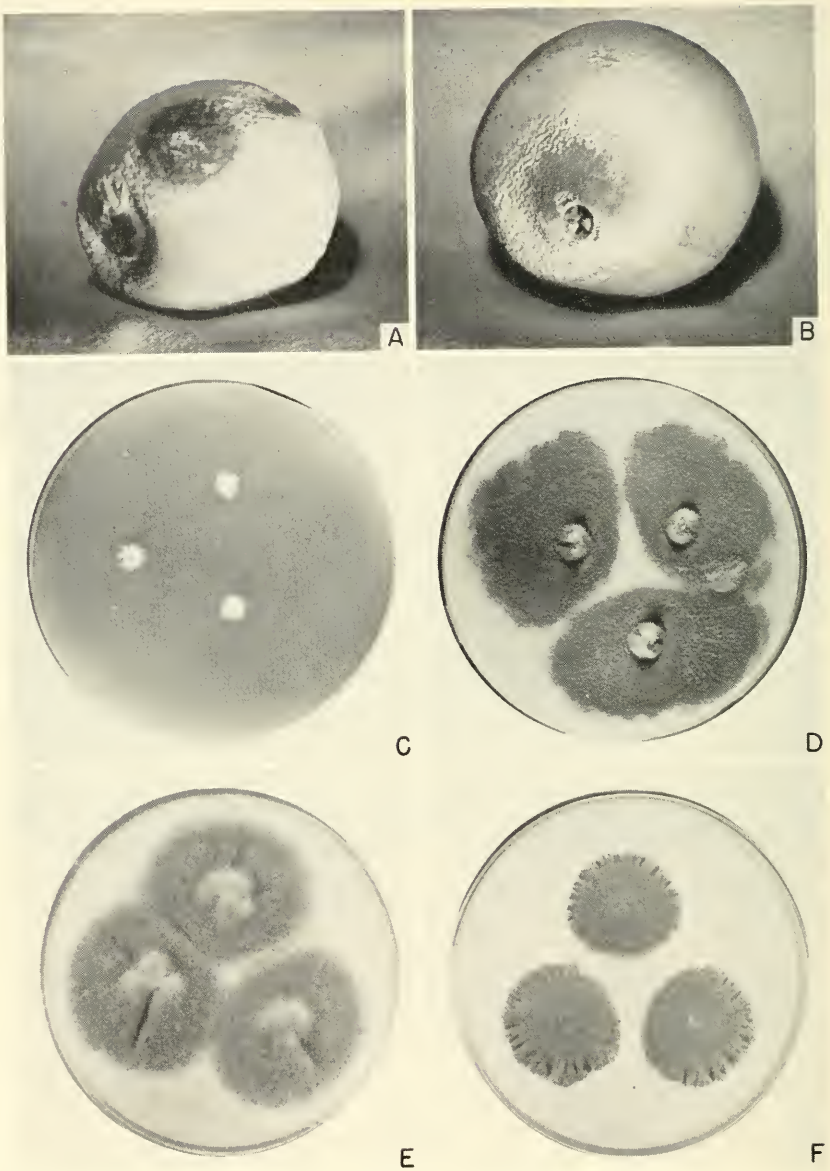


FIG. 103. *Penicillium digitatum* Saccardo. *A* and *B*, Species occurring as a natural infection upon lemon and orange, respectively. *C* and *D*, NRRL 1202 on Czapek and steep agars at two weeks. *E*, Floccose, spreading variant of NRRL 786 on steep agar. *F*, More restricted, heavier sporing variant of same strain, also on steep agar.

that are typically elliptical but may show wide individual variation; conidial chains vary greatly in length, up to 150μ, usually divergent and commonly becoming entangled with other chains from the same or adjacent penicilli; conidiophores typically very short, commonly ranging from 30 to 100μ by 4.0 to 5.0μ, smooth-walled (although granular appearing hyphae are occasionally observed under oil), arising from submerged hyphae, or from the basal mycelial felt in colonies upon malt or other nutrient-rich media; penicilli typically biverticillate and asymmetrical but varying greatly in dimensions and complexity (fig. 102), rarely appearing monoverticillate or unbranched, with branches, metulae, and sterigmata often poorly defined; consisting of branches varying greatly in length and bearing either metulae and sterigmata, or sterigmata only; metulae variable in form and dimensions, commonly ranging from 15 to 30μ by 4.0 to 6.0μ and bearing sterigmata in variable but always limited numbers; sterigmata equally variable and ranging from 15 to 28μ by 3.5 to 5.0μ, usually producing chains of elliptical conidia, but occasionally terminating in swollen vesicular cells; conidia smooth-walled, dull dark green in mass, varying greatly in form and dimensions (fig. 102), ranging from subglobose to long cylindrical in shape but usually elliptical, commonly 3.5 to 5.0μ by 3.0 to 3.5μ at first, then 6.0 to 8.0μ by 4.0 to 6.0μ and occasionally up to 10 to 12μ by 6.0 to 8.0μ with substantial differences in form and dimensions of conidia commonly occurring within the same chain.

The above description is based primarily upon NRRL 786 (Thom's No. 176), isolated by Thom in 1904 at Storrs, Connecticut, which has been maintained continuously in laboratory culture since that time and which has been checked against Saccardo's exsiccati, a portion of orange peel, distributed in 1880. The species is represented also by NRRL 1202 and NRRL 1203 isolated in 1940 from a lemon and an orange respectively at the Northern Laboratory, and numerous strains more recently isolated from spoiling citrus fruits in connection with the present study. A culture received from the Centraalbureau under this name was entirely typical.

Experience indicates that the description as presented will adequately cover all but an occasional member of this series as they are isolated from fruits collected from packing plants, storage warehouses, and consumer markets in this country and abroad. Occasional variants are encountered. One such form producing white conidia and showing no green color was sent to Thom in 1924 by Dr. H. S. Fawcett, Riverside, California, and in Thom's Monograph (1930, p. 245) was cited as a new variety, *Penicillium digitatum* Sacc. var. *californicum*. Less striking variants are commonly observed, and forms characterized by more or less restricted (fig. 103F) rather than broadly spreading colonies (fig. 103E), when grown upon malt extract or other nutrient rich media, can be separated from almost any

normal culture by deliberate strain selection. Fruiting structures in such forms generally remain unchanged.

Saccardo's specimen in Fungi italici, No. 894, was examined by Thom and is near enough to type material to establish the identity of Saccardo's species with certainty. A strain was collected in Hanover, Germany by Thom and verified by Professor C. Wehmer as representing the latter's *Penicillium olivaceum*, hence synonymous with *P. digitatum*. Other cultures examined have been contributed by numerous investigators in this country and abroad. There seems to be no question but that this species, along with *P. italicum*, can be obtained from oranges, lemons, etc., wherever these citrus fruits are grown, handled, or consumed.

A considerable number of species and varieties, undoubtedly synonymous with *Penicillium digitatum* Sacc., have been described. Of these, only *P. olivaceum* Wehmer is cited in the literature commonly enough to warrant special comment; others are considered only in the species index.

Penicillium olivaceum Wehmer, in Beitr. z. Kentn. Einh. Pilze, II, pp. 73–76; Taf. I. fig. 2, Taf. II, fig. 11–15; Jena. 1895. Thom, The Penicillia, p. 245. 1930. Wehmer's description and figures of this species are good and his name for it is so apt and descriptive that it is unfortunate that it must be replaced by that given by Saccardo which was considered and refused by Wehmer for members of this group. Our conception of the species was obtained from cultures made directly from rotting oranges in Wehmer's laboratory and compared to specimens actually distributed by Saccardo, thus leaving no room for doubt as to identity. Wehmer's species is synonymous with *P. digitatum* Saccardo.

Penicillium digitatum Saccardo var. *californicum* Thom, in The Penicillia, p. 245. 1930

This variety was based upon a strain which produced white conidia and an entire absence of green color. It was received in May 1924, from H. S. Fawcett, Riverside, California who reported it to be equally as destructive of oranges as the usual olive green form. The strain was soon lost from Thom's Collection and has not again been reported. The occurrence of white or tan variants has been observed in many species, and the strain upon which Thom based his variety was undoubtedly of such origin.

Penicillium nivcum Sopp (Monogr. pp. 182–184, Taf. XXIII, fig. 16. 1912; Thom, The Penicillia, p. 242. 1930) was compared with *P. digitatum* Sacc. by Sopp, but close relationship is doubtful. Colonies were described as white with penicillate conidial structures, long tapering sterigmata, and abundant conidia 9 to 18 to 20μ. The species might possibly have represented some form approximating *P. digitatum* Sacc. var. *californicum* Thom.

Occurrence and Significance

Penicillium digitatum Sacc. has been widely studied because of the destructive olive-green rot of citrus fruits produced by it. As one would ex-

pect, most of these studies have centered upon ways and means of reducing or preventing this rot. As early as 1908, Powell, *et al.*, in the U. S. Department of Agriculture, showed that the mold, while always present in citrus producing areas and hence common on the mature fruit, entered as a wound parasite and was unable to penetrate sound fruit. The importance of careful handling in harvesting, storage, and marketing the fruit was recognized and the system of distribution was altered to effect great reductions in losses due to green rot. Subsequent to this Shiver, Fulton, and Bowman (also of the Department of Agriculture) demonstrated that losses could be further reduced by washing the fruit in boric acid or borax solutions. The practice has been widely adopted in this country and abroad. Nattrass (1935), working in Cyprus, reported fruits dipped in cold saturated borax solution or in 1 per cent "shirlan" (cold) to remain almost free of infection. Tzereteli and Tchanturia (1939) found an 8 per cent solution of borax to give good control in the Georgian Soviet Republic. Tompkins and Trout (1932), in laboratory experiments, successfully reduced losses by storing fruit in air containing low concentrations of acetaldehyde or ammonia. An ammonia concentration sufficient to prevent mold growth was developed by the dissociation of ammonium bicarbonate crystals. Nattrass (1935) and Tchanturia and Tzereteli (1940) have suggested the use of iodine preparations to combat *P. digitatum* and *P. italicum* infections. Childs and Siegler (1946) used thiourea and thioacetamide in 5 per cent aqueous solutions and quinosol in 8 per cent solutions for momentary dips. Losses in some varieties were reduced from 40 per cent to 2 per cent or lower. Gioelli (1932) reported marked differences in susceptibility of fruits produced on plots receiving different fertilizers. Fruit from areas receiving potash only or iron sulfate rotted less rapidly than those from plots receiving nitrogenous fertilizers.

Fulton (1929) investigated the effect of ultraviolet radiations on 27 species of fungi, including *Penicillium digitatum*. An exposure of five seconds at 6 inches killed 907 out of 1000, whereas an exposure of 45 seconds killed 998 out of 1000 spores of this species when spread on the surface of agar plates. Spores on the surface of citrus fruits were likewise killed without apparent injury to the fruit. Decay of inoculated fruits was only moderately reduced by exposure to ultraviolet, however, since the light could not kill spores in areas accidentally shaded or penetrate the rind to destroy mycelium already beginning to grow.

Exposure to ethylene gas has, for a considerable time, been known to hasten the coloring process in citrus fruits (Denny, 1924). Further, it was commonly observed that the fruit in a crate containing scattered fruits rotting with green mold appeared to "ripen" faster than in like crates containing only sound fruit. It was not until 1940, however, that Biale (Univ.

of Calif.) and Miller, *et al.* (U.S.D.A.) discovered independently that ethylene was evolved by citrus fruits, and that decaying fruits produced more than sound ones. It was further shown in both investigations that *Penicillium digitatum* is capable of producing ethylene, thus further hastening the coloring process.

Penicillium digitatum grows very poorly upon Czapek's solution agar and other "synthetic" media, but grows luxuriantly upon "natural" substrata such as malt and potato-dextrose agars. In our experience, *P. digitatum* has often been observed to grow luxuriantly upon Czapek agar in plates contaminated with other mold fungi. An explanation of this behavior is found in the work of Wooster and Cheldelin (1945). Studying the nutrition of *P. digitatum* under carefully controlled conditions, these investigators found that thiamin, or the thiazole moiety, was required, and that a quantitative increase in growth could be obtained over a range from 0.01 to 3.0γ/25 ml. of culture solution. Other vitamins, including pyridoxine, pantothenate, and biotin were stimulatory. Glucose afforded a more favorable carbon source than sucrose (which is commonly used in Czapek's agar), and organic nitrogen sources such as asparagine or hydrolyzed casein were better than $NaNO_3$ and other inorganic salts. Elze (1934) reported *P. digitatum* to grow more luxuriantly and to be more virulent in the presence of *Diplodia natalensis* than when inoculated into oranges singly A synergistic effect was observed between *P. digitatum* and *Oospora citri-aurantii* in laboratory cultures by Gemmell (1939), who demonstrated also that these fungi produced more rapid and extensive rotting of fruit when inoculated together than when either one or the other was present as the sole pathogen.

Birkinshaw, Charles, and Raistrick (1931) have reported limited biochemical studies on *Penicillium digitatum.* Considerable ethyl acetate was produced from glucose, and in addition some ethyl alcohol and a new polysaccharide which gave rise to glucose upon hydrolysis.

Penicillium roqueforti Series

(Roquefort-type Cheese Molds)

Outstanding Characters

Colonies usually but not always broadly spreading, velvety, azonate, generally thin, with abundant short conidiophores arising from trailing hyphae or submerged hyphae just below the agar surface, growing margin commonly appearing arachnoid or cobwebby, conidial areas typically in dark yellow-green shades, often showing greenish to almost black shades in colony reverse.

Conidiophores conspicuously roughened or tuberculate in aerial portions, with cellular elements of the penicillus often similarly roughened.

Penicilli asymmetrical, irregularly branched, bearing conidia in long tangled chains or adherent in loose columns.

Conidia comparatively heavy-walled and smooth, appearing dark yellow-green when viewed under high magnifications.

Series Key

2. Conidiophores typically rough-walled; colony margins usually appearing arachnoid ..... *P. roqueforti* series
   a. Colonies broadly spreading, with surface plane or nearly so, margins thin, typically appearing arachnoid ..... *P. roqueforti* Thom
   b. Colonies restricted, strongly wrinkled or furrowed, margins hardly arachnoid. *P. casei* Staub

Members of this series are the predominant molds in the whole group of cheeses characterized by streaks, or "marbling", of green mold (fig. 105A). Closely related strains appear in the true Roquefort, or sheep's milk cheese of southern France, in the "fromages bleus" of central France, made from either sheep's milk or cow's milk, in Gorgonzola as made in northern Italy, in Stilton as made in England, in Gammelost as made in Norway, in Blue cheese or American Roquefort as made in the United States, and in many less well-known varieties of loose-textured cheeses which obtain their characteristic flavor and appearance from the molds which line the channels and cracks throughout their mass. Members of this series are likewise the dominant molds found in spoiling ensilage, and appear fairly frequently in miscellaneous cultures from food products and soils.

In contrast to the Camembert type cheese molds, which are deeply floccose, white or nearly so, and grow only on the surface of the pressed milk curd, members of the *Penicillium roqueforti* series represent velvety, dark green forms which invade the holes and cracks in loose-textured cheeses. In manufacturing such cheeses as Roquefort, Gorgonzola, Stilton, etc., the curd is so managed as to leave cracks, channels and openings between the particles as they are pressed together. The "marbling" characteristic of such cheeses when ripe results from the growth and sporulation of the mold throughout the network of interconnecting channels. In studying these cheeses, Thom and Currie (1913) showed that these channels and spaces within the cheese contained less oxygen than atmospheric air, and that the Roquefort mold dominated the flora of these spaces because of its ability to grow in gas mixtures containing as little as 5 per cent oxygen.

Members of the *Penicillium roqueforti* series, as it is now understood, have been studied particularly with relation to their role in cheese manufacture.

Sopp, publishing under the name of Johan-Olsen (1898), appears to have been one of the first to suspect the importance of these molds, as evidenced by his isolation and discussion of them under such designations as *P. aromaticum casei*, *P. aromaticum* "I" and "II", "Gammelost", and "Roquefort". He failed, however, to describe these adequately, and he declined to distribute cultures to other investigators working in similar fields elsewhere. While closer identification is impossible under the circumstances, we can safely assume that he was dealing with members of the *P. roqueforti* series showing the usual range of strain variation. His subsequent Monograph on *Penicillium* (1912) did little to clarify his earlier confusing nomenclature.

Dierckx in 1901 published his brief description of *Penicillium atro-viride*, based upon a mold which Biourge (1923) subsequently held to be the same as *P. roqueforti* Thom. Dierckx's description was, however, too inadequate for subsequent recognition.

Thom (1906) was the first to conclusively demonstrate the significance of these molds in cheese production, and was likewise the first to present an adequate description of the responsible species. Hence, *Penicillium roqueforti* Thom has come to be generally recognized as the principal species directly concerned with the production of cheeses of the Roquefort type, and constitutes the center around which the present series is based.

Biourge maintained that Dierckx had intended *Penicillium atro-viride* to include all the fungi connected with the production of such cheeses as Roquefort, Gorgonzola, etc. He added further that if a collective name could be applied to the whole series of closely related strains, it should be *P. atro-viride* rather than *P. roqueforti* Thom. However, since no one has been able to decide from his description just what type of organism Dierckx intended by his *P. atro-viride*, the name may be justly dropped except for its possible historical interest. Biourge applied the name Stellata to this general series to emphasize the contrast between the smooth, even or regular margin of the colonies of *P. chrysogenum* and its allies (his Radiata) and the more or less uneven or irregularly developing colonies of *P. roqueforti* and related species. Whereas the name is somewhat applicable, it seems to us to exaggerate the appearance actually encountered. Furthermore, the development of a more or less stellate pattern is not confined to this single series of molds as Biourge implied.

Biourge (1923), Arnaudi (1928), Bainier (1907), and others have described additional species and varieties closely related to *Penicillium roqueforti* upon the basis of cultures isolated from other named cheeses of the Roquefort type or upon the cultural characteristics of individual strains. Examination of their descriptions and figures, and in most cases comparison of their type strains as well, has failed to show differences beyond those

anticipated among strains in cosmopolitan and variable species such as *P. roqueforti*, hence, in our opinion, do not warrant continued recognition. Identification of newly isolated cultures with one of the species descriptions published by Sopp, Weidemann, Bainier, or Biourge is scarcely probable. However, these descriptions may be illuminating as emphasizing the range of variations found within the series, since in a general way they characterize more or less definite members of a variable series of related organisms.

The series embraces only one well-defined species in addition to *Penicillium roqueforti* Thom, namely: *P. casei* Staub. This latter species is rather frequently encountered as an infection of the rind of Swiss and related cheeses where it produces small areas of brownish discoloration. In agar plate cultures it shows the general characteristics of the series in the pattern and markings of conidial structures but consistently produces more restricted colonies with less arachnoid margins than strains of *P. roqueforti* Thom.

Penicillium roqueforti Thom, in U. S. Dept. Agr., Bur. Anim. Ind., Bul. 82, pp. 35–36, fig. 2. 1906. Also *ibid.*, 118, p. 34, fig. 4. 1910; and The Penicillia, pp. 277–279, fig. 38. 1930

Colonies on Czapek's solution agar (Col. Pl. VI) spreading broadly, attaining a diameter of 5.0 to 6.0 cm. in 10 to 12 days at room temperature, heavy sporing, velvety with surface fairly smooth or plane, with margin broad, white, thin (fig. 105B), cobwebby or veil-like (arachnoid) with hyphae radiating partly on the surface and partly just below the surface of the substratum, and green conidial areas following the hyphae in unevenly radiating lines (constituting the basis of Biourge's section Stellata), forming a mass 100 to 300μ deep, at margin white then bluish green near gnaphalium green or pea green (Ridgway, Pl. XLVII) and then quickly dull green near Russian green (R., Pl. XLII); no exudate produced in most strains; odor not characteristic or pronounced, slightly sour or moldy; reverse in shades of green or bluish green to almost black, varying with conditions of culture and often in different sectors in the same colony; penicilli variable in pattern from simple monoverticillate structures (fig. 104B_3), to verticils of metulae and sterigmata, or compact branching systems, with one or more long appressed or diverging branches (fig. 104B_1 and $_2$), sometimes giving a cymose appearance, bearing conidia in long tangled chains or forming loose columns (fig. 104A); conidiophores mostly short, usually about 100 to 150μ, less frequently up to 200μ long by 4.0 to 6.0μ in diameter, ascending from aerial loops or submerged sections of vegetative hyphae, often branched, with walls granular from encrustments or protuberances of variable size (occasionally smooth) (fig. 104B); metulae 12 to 15μ by 3.0 to 4.5μ, mostly with walls more or less roughened or asperulate (fig. 104B); sterigmata 8.0

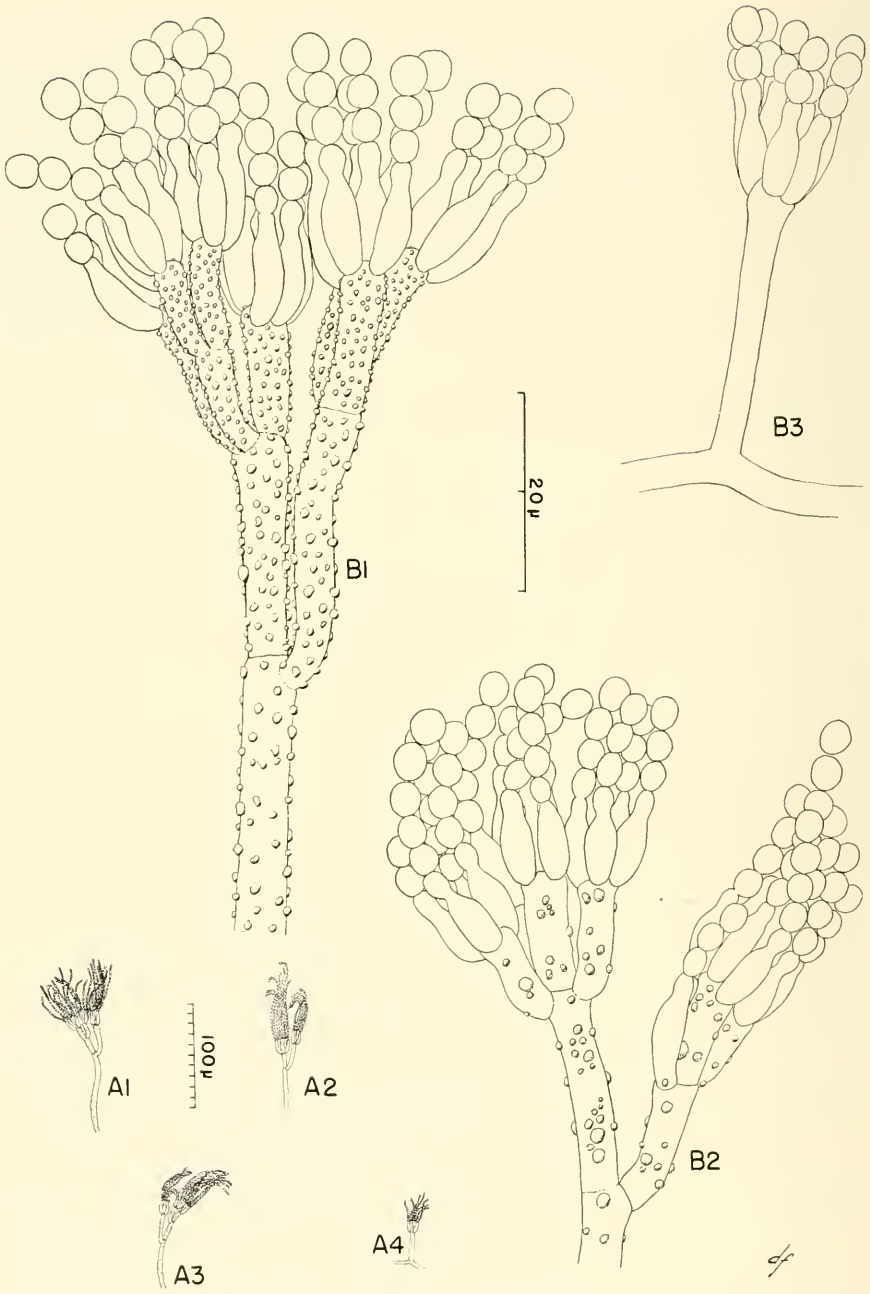


FIG. 104. *Penicillium roqueforti* Thom. A_1–A_4, Habit sketches of representative penicilli. B_1–B_3, Detailed drawings showing penicilli of varying complexity. Conidiophore walls are usually conspicuously roughened or tuberculate, but may be smooth, particularly in smaller structures like B_3.

to 12.0μ by 3.0 to 3.5μ; conidia globose or subglobose, commonly ranging from 3.5 to 5.0μ, not infrequently larger up to 7.0 or 8.0μ, smooth-walled, dark green in mass.

Colonies on steep agar essentially duplicating those upon Czapek in color, cultural characteristics, and details of morphology, but growing somewhat more rapidly; penicilli as described above.

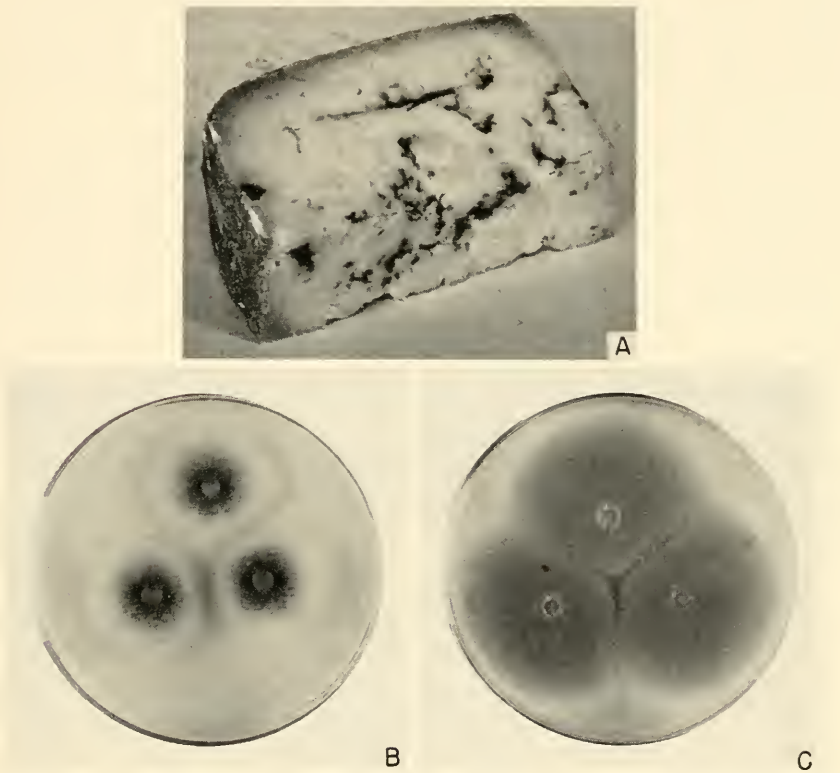


FIG. 105. *Penicillium roqueforti* Thom. *A*, Piece of Roquefort cheese showing characteristic marbling (dark green) due to growth of the mold in channels throughout the cheese. (After Thom, in Jour. N. Y. Bot. Garden *45*, 1944.) *B* and *C*, Ten-day old colonies of NRRL 849 (type) on Czapek and malt agars.

Colonies upon malt extract agar growing more rapidly than on Czapek, attaining a diameter of 8.0 to 10.0 cm. in 8 to 10 days (fig. 105C), but otherwise similar in basic character and coloration; reverse becoming blackened in age; conidiophores and metulae usually exhibiting increased roughness and conidia tending to form longer and more compact columns up to 200 or 300μ in length.

Species description is based upon Thom's type, his No. 18 (NRRL 849),

isolated originally from French Roquefort cheese in 1904, and numerous other strains possessing similar cultural and morphological characteristics that have been isolated by the authors or received from collaborators over a period of many years. Among such cultures now contained in our Collection may be mentioned NRRL 850, received in 1930 from Dr. W. T. Johnson, Grove City, Pennsylvania; NRRL 852 from the same source in 1933; NRRL 853 from Professor F. D. Heald, State College of Washington in 1930; NRRL 854 from Dr. Paul Simonart, brought by him from Biourge's Laboratory in 1936; NRRL 858 from Biourge as his *Penicillium gorgonzola;* and a number of strains received in 1943 from Dr. E. R. Hiscox, National Institute for Research in Dairying, North Reading, England.

Other strains contained in this Collection fail to duplicate NRRL 849 and similar forms in all particulars, but do not differ from them sufficiently to warrant separate recognition. These include: NRRL 851, received in 1940 from Dr. M. M. Harris, Waycross, Georgia; and NRRL 1168, received in 1940 from Dr. G. A. Ledingham, Ottawa, Canada. Both of these produce colonies with denser and less arachnoid margins, are usually heavier sporing, show a brighter green coloration in conidial areas ranging from pistachio green to dark American green (R., Pl. XLI), and run toward dark brown rather than dark green or greenish black in colony reverse. A culture received from the Centraalbureau in May 1946 as the type of *Penicillium roqueforti* var. *viride* Dattilo-Rubbo shows the same bright yellow-green colors and general cultural characteristics of the above. Variants of this type are fairly common, but lack sufficient bases for specific, or varietal recognition.

Other strains, not complying with either of the above groups, include: NRRL 857, received from Biourge as *Penicillium gorgonzola* Weidemann; NRRL 855, from Dr. Paul Simonart as Biourge's culture No. 156; and NRRL 1165, isolated from waste sulfite liquor by G. A. Ledingham, Ottawa, Canada. These cultures produce almost floccose, sparsely sporing colonies which are light blue-green in color and show little or no color in reverse. Recognition of *P. gorgonzola* to include cultures of this type is not warranted since the strains involved show only quantitative differences in spore production and development of aerial hyphae from typical *P. roqueforti* strains, and since cultures of this particular type are not claimed to be especially significant in the production of Gorgonzola cheese.

While considerable variation characterizes the different members of the *Penicillium roqueforti* series, it is interesting to note that, unlike cultures of *P. oxalicum* (p. 378), specific strains usually remain stable over long periods of time in laboratory culture. Strain NRRL 849 (Thom's No. 18), for example, duplicates in all essential characters the appearance and mor-

phology of this culture as it was isolated by Thom from French Roquefort cheese more than 40 years ago.

Thom's original description of *Penicillium roqueforti* was prepared before the multiplicity of strains and variations in this series was appreciated. By emending his *P. roqueforti* description of 1906, Thom, in 1930, recognized the inadequacy of that description together with the pertinence of criticisms by Westling (1911), Weidemann (1923), and Biourge (1923). We continue to believe that the student of these molds is better served by broadening the description of *P. roqueforti*, which is widely used in the cheese industry, than by recognizing additional species to cover the cheese molds used in particular localities for the ripening of cheeses of the Roquefort type. Considering the number of intergrading forms that are encountered, hundreds of which have been handled, we doubt whether any worker can positively separate *P. gorgonzola* Weidemann, *P. stilton* Biourge, etc., from *P. roqueforti* Thom in comparative cultures in the laboratory.

Many species and varieties, obviously belonging to the series with *Penicillium roqueforti* Thom, have been described without characteristics sufficiently unique to separate them from *P. roqueforti* in the broad sense of this Manual. Some of these were based upon individual strain characteristics, others upon the particular named cheese from which the mold was obtained or for the manufacture of which it was employed, and still others resulted from the describers' lack of information regarding the published literature. A partial list of such species and varieties follow; others may be found only in the Species Index.

Penicillium roquefort Sopp, in Monogr. pp. 156–157, Pl. XVII, figs. 118 and 119 and Pl. XXII, figs. 7 and 8. 1912. Sopp proposed the name *P. roquefort*, citing the same figure that he used for *P. aromaticum I* (Roquefort) on the preceding page. His figures do not fit any strain of *P. roqueforti* so far examined, though his vernacular notes establish the presumption that the mold of Roquefort cheese was in his laboratory. Considering all the circumstances, *P. roqueforti* of Thom's 1906 paper is left as the earliest fully verifiable description. *Penicillium aromaticum I* (Roquefort) used by Sopp (O. Johan-Olsen, in Centbl. f. Bakt. etc. (II) **4**: 161–169. 1896) can Hardly be used to justify *P. roquefort* as the accepted name.

Penicillium roqueforti Thom var. *weidemanni* Westling, in Arkiv för Botanik **11**: 52, and 71–73; figs. 6 and 49. 1911. Westling merely added reverse of colony green or dark green to Thom's original diagnosis of the species. This emendation was made in a subsequent description of the species *P. roqueforti* Thom, since it is characteristic of the type and other representative strains.

Penicillium atro-viride Dierckx, in Soc. Scient. Brux. **25**: 87. 1901. See also Biourge Monogr. p. 199. 1923. Biourge, with access to Dierckx's unpublished notes, expressed the belief that Dierckx's species name should be applied to the series. He paid no attention to the fact that no intervening worker had ever identified the cheese

mold by Dierckx's description. The species name may better be dropped because the author failed to describe his material properly.

Penicillium atro-viridum Sopp, in Monogr. pp. 149–150, Taf. XVI, fig. 114; Taf. XXIII (XXII corrected) fig. 12. 1912. Sopp's specific name was apparently offered independently of *P. atro-viride* Dierckx (1901). It is probably based upon one of the *P. roqueforti* series producing very dark conidial areas and very dark greenish black reverse. Sterigmata were reported as large, flask-shaped, and to produce globose or angular conidia 4.0 to 6.0μ in diameter. His culture has not been seen by anyone else.

Penicillium vesiculosum Bainier, in Bul. Soc. Mycol. France **23:** 10–12, Pl. II, figs. 1–8. 1907. Bainier described a strain with all cells swollen and containing large vacuoles in the mycelium, conidiophores, and penicilli. The structures reported and illustrated were obviously pathological. Occasional strains of the *P. roqueforti* series show structures resembling those described. We believe his species to have been based upon such a strain.

Penicillium aromaticum ("Gammelost") Sopp, in Monogr., pp. 159–161, Taf. XVII, fig. 123; Taf. XXII, fig. 10. 1912. Sopp offered this as a change of name for *P. aromaticum II*, a yellow-green mold included in his earlier discussion of cheese molds (Centbl. f. Bakt. etc. (II) **4:** 161–169. 1898). In spite of his statement that this was different from the Roquefort culture, no data were given which would remove it from the *P. roqueforti* series. Sopp did not distribute cultures and his species is known by description only.

Penicillium gorgonzola Weidemann, in Biourge, Monogr., La Cellule **33:** fasc. 1, pp. 204–206; Col. Pl. V and Pl. VIII, fig. 43. 1923. Biourge identifies this species with *P. roqueforti* var. *weidemanni* Westling (see above), hence assignment of the name appears to be arbitrary. Biourge reported that his culture grew poorly upon potato in contrast to good growth of *P. roqueforti*. Reporting on the same culture, Thom (1930) described colonies as broadly spreading, velvety, 200 to 300μ deep with uneven arachnoid margin, conidial areas in pale bluish then bluish green, reverse uncolored, with conidiophores short and roughened, conidia subglobose, about 4.0 to 5.5μ in diameter. Current examination of Biourge's strain, NRRL 857, in general confirms Thom's observation and fails to show sufficient bases for separation as either a species or variety. No significant relation to Gorgonzola cheese was claimed.

Penicillium stilton Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 206–207; Col. Pl. V and Pl. VII, fig. 42. 1923. Biourge, with only a few strains in the group before him, applied this name to one isolated from Stilton cheese, a cheese of the Roquefort type made from cow's milk and taking its name from the town of Stilton, England. Colonies of Biourge's culture growing upon Czapek's agar showed more floccosity, less green color due to reduced conidium production, and little or no color in reverse. It grew poorly on potato. Among the multitude of variants seen within the series, forms which seemed to reproduce this characterization closely have been seen occasionally; but intermediate forms are too commonplace to justify maintaining *P. stilton* as a separate species.

Penicillium suavolens Biourge (Monogr., La Cellule **33:** fasc. 1, pp. 200–202; Col. Pl. V and Pl. VIII, fig. 4. 1923) as known from the original description and from Biourge's culture sent to Thom in 1924, represents a member of the *P. roqueforti* series characterized principally by the production of paler green colors, shorter conidio-

phores, and reverse in comparatively light yellow to brownish rather than greenish to black shades. Recognition of a separate species is believed unwarranted in view of the strain variation characteristic of the *P. roqueforti* series.

Penicillium biourgei Arnaudi (Boll. Ist. Sieroterapico Milanese **6:** fasc. 1, pp. 25–27, Pls. 1–2, 1927; also Centbl. f. Bakt. etc. (II) **73:** 321–330. 1928), as originally reported and described seemed to represent a member of the *P. roqueforti* series which the describers found to be significant in the ripening of Gorgonzola cheese. A strain received from the Centaalbureau in February 1946 under this name and presumably type, since it came originally from the Institute Sieroterapico in Milan, clearly belongs with *P. roqueforti* Thom, differing only in producing more prominent and lighter sporing radial sectors than most strains. The comparative studies of Arnaudi included fourteen races of mold found in cheese, all of which apparently belonged to the *P. roqueforti* series.

Penicillium casei Staub, in Centbl. f. Bakt. etc. (II) **31:** 454–466, 1911; Thom, The Penicillia, p. 270. 1930

Colonies on Czapek's solution agar restricted, 2.0 to 2.5 cm. in diameter in 2 weeks at room temperature, buckled and wrinkled, with marginal area deeply dissected by 4 or more radial furrows, somewhat zonate, velvety, heavily sporing, growing marginal zone 1.0 to 1.5 mm. wide, white, shading into fairly bright yellow-green shades from asphodel green through pois green to leaf green (Ridgway, Pl. XLI); exudate limited, light yellow, mostly in central colony areas; odor very faint or lacking; reverse in yellow to orange, brown, or almost black shades, with the color somewhat diffused into the surrounding agar; conidiophores borne in a dense stand, arising mainly from a closely interwoven and tough basal mycelial felt, mostly 150 to 200μ in length by 3.0 to 4.0μ, but ranging from 100 to 250μ, with walls usually conspicuously roughened; penicilli asymmetric, irregularly branched, with spore bearing apparatus variable in length from 20 to 60μ but mostly 40 to 50μ, typically consisting of one or more branches in addition to the main stem, each terminating in a cluster of metulae bearing sterigmata and spore chains at first adhering into poorly defined columns but later appearing as an irregular tangled mass up to 50μ or more in length; branches variable in size, mostly 12 to 20μ by 3.0 to 4.0μ, occasionally rebranched; metulae borne in groups of 3 to 5, mostly 7.0 to 12.0μ by 2.5 to 3.5μ; sterigmata in small clusters, mostly 7.0 to 9.0μ by 2.2 to 2.7μ with longer individuals occasionally borne at the level of the metulae; conidia subglobose to broadly elliptical, 3.0 to 3.5μ in long axis, smooth-walled, yellow-green *en masse*.

Colonies on steep agar growing more rapidly, attaining a diameter of 3.0 to 3.5 cm. in 2 weeks at room temperature, closely and conspicuously furrowed in a radial pattern, heavily sporing, in color and general texture duplicating colonies on Czapek agar; penicilli generally somewhat larger

than above but of similar pattern; conidiophore walls generally less definitely roughened.

Colonies on malt agar very restricted, about 1.5 cm. in 2 weeks, velvety, heavily sporing, colored as on Czapek; no exudate; penicilli of the same basic pattern as above but more compact and somewhat coarser, with conidiophores consistently heavier, up to 4.5 to 5.0μ in diameter and very conspicuously roughened.

Species description based primarily upon NRRL 844, Thom's No. 5056, isolated from Swiss cheese. The species is believed to be widely distributed since representative strains have been repeatedly isolated from brown spots on the rinds of Swiss and other related cheeses. While cultures are not difficult to maintain in the laboratory, they tend to die out more rapidly than many of the Penicillia, hence should be transferred more frequently than most.

Penicillium casei Staub shows the general characters of the *P. roqueforti* series sufficiently to be included here more satisfactorily than elsewhere. It differs from the more common molds of the *P. roqueforti* type, however, in producing more restricted and slowly growing colonies and in failing to show the broad arachnoid margin characteristic of that species. The conidial structures of the two species are strikingly similar.

Occurrence and Significance

The distribution of *Penicillium roqueforti* in nature is largely determined by its physiological characteristics. It is able to grow under quite acid conditions and in an atmosphere of low O_2 concentration. Hence, it commonly appears in the mycoflora of surface layers in fermenting ensilage, and is the dominant mold found in cheeses of the Roquefort type. Its almost universal use in the manufacture of the latter products rests, not only upon its ability to grow deep into the loosely pressed curd, but more particularly upon the enzymes which it produces and the flavors that are developed through the action of these upon the fatty and proteinaceous milk constituents.

Roquefort and other cheeses of the same general type have long been produced in various parts of Europe, and limited studies of a mycological nature were early made by Johan-Olsen (Sopp) in Norway (1898), by Dierckx in Belgium (1901), and by Bainier in France (1907a). Production methods, however, were largely empirical, and the manufacture of high quality cheeses resulted from a combination of unique climatic conditions and the successful establishment of a flora in which the mold now known as *Penicillium roqueforti* represented the dominant species.

Real advances toward controlled production and an understanding of critical microbiological processes were made when Thom and co-workers successfully introduced the manufacture of Roquefort-type cheeses in this country. Thom isolated a particular kind of mold regularly from the better imported cheeses, and in 1906 described the form as *Penicillium roqueforti*. Subsequent studies by Thom and Currie (1913) revealed sound physiological bases for the dominance of this mold, and to a large degree elucidated its role in cheese production. The mold was found to tolerate high salt concentration in an acid environment, to grow in an atmosphere containing as little as 5 per cent oxygen, and to produce abundant lipolytic and proteolytic enzymes. Currie (1914) concluded that the presence of caproic, caprylic, and capric acids, resulting from fat hydrolysis by water-soluble lipase produced by the mold, were largely responsible for the characteristic flavor of Roquefort cheese. Additional studies in the U. S. Department of Agriculture were made by Matheson and others after Thom and Currie turned to other fields.

A marked revival of interest in Roquefort-type cheeses has occurred in the United States during recent years, and successful research programs have been conducted in several laboratories. Those at the University of Minnesota and at Iowa State College have been among the most active and productive, and have contributed substantially to the establishment of a limited but successful industry in that area. No attempt will be made to present a complete bibliography, or to review the numerous significant contributions that have been issued by these and other laboratories. However, a considerable list of titles is included in the Topical Bibliography (see p. 723), and from these the interested reader can obtain a reasonably comprehensive knowledge of the subject. As a partial guide to this literature, the following facts may be noted: Golding, in a series of papers from 1926 to 1945, investigated particularly the nutritional requirements and gas relationships of *Penicillium roqueforti*. Gottlieb (1946) studied the utilization of amino acids as a source of carbon by *P. roqueforti*. Hammer, Lane, Bryant, Jensen, and others at Iowa State College have investigated various factors affecting cheese manufacture, particularly flavor development. Macy, Thibodeau, Coulter, Combs, George, and others at Minnesota have likewise studied factors influencing production, with special emphasis on enzymatic changes and the influence of acidity. Tomasi (1928), Bryant and Hammer (1940), Funder (1946), and others have analyzed the microflora of Roquefort-type cheeses as this relates to production, quality, and storage.

Ayres and Niedercorn received a patent (U. S. 2,278,236, March 31, 1942) covering the production of proteolytic enzymes by cultivating *Peni-*

cillium roqueforti upon moist bran, which was then dried after the enzyme content reached a maximum.

Irvine and Sproule (1940) and Willingham (1941) reported propionic acid to be an effective inhibitor of molds in dairy products, including cheese. Salts of this acid were less effective.

Penicillium brevi-compactum Series

Outstanding Characters

Colonies usually restricted, typically consisting of a close-textured felt, with surface growth velvety to almost lanose, often conspicuously furrowed, heavy sporing, in dull yellow-green to gray-green shades, reverse usually in dull yellow, greenish gray, or brownish shades.

Conidiophores variable in length, with longer individuals borne from the substratum and shorter stalks borne as branches from aerial hyphae, smooth or somewhat roughened.

Marginal stolons typically produced in all members of the series, especially when cultivated upon moist substrata or under very humid conditions.

Penicilli asymmetric, typically branched, short and compact with branches appressed, metulae and sterigmata numerous and closely crowded; in some strains unbranched, consisting of a compact terminal cluster of metulae bearing crowded sterigmata.

Conidia subglobose to more or less pyriform or elliptical, smooth or delicately roughened, borne in fairly long tangled chains.

Series Key

B. Penicilli comparatively short, compact, with all elements closely appressed. *P. brevi-compactum* series

1. Penicillus typically showing one or more side branches below the level of metulae.
   a. Conidiophores coarse, with branches and metulae commonly inflated. *P. brevi-compactum* Dierckx
   b. Conidiophores thinner, flexuous, with branches and metulae not inflated. *P. stoloniferum* Thom
2. Penicillus typically consisting of a single, crowded terminal verticil of 5 to 8 metulae..... *P. paxilli* Bainier

Members of this series are encountered among isolates from all soils examined. While comparatively abundant, they do not, because of their slow and limited growth, attract the immediate attention commanded by more rapidly growing and more highly colored members of other series. They commonly occur upon decaying vegetation, nuts, fruit, paper stocks, etc., and seem to be somewhat selective of fleshy fungi as habitats. Thom's type of *Penicillium stoloniferum* was isolated from such a source; Bainier's *P. paxilli* was based upon an isolate from a moldy *Paxillus*, hence the name;

and numerous strains in our possession have come from decaying fleshy fungi of one type or another.

This series is characterized particularly by the comparatively short and very compact base of the penicillus. Typically this consists of a compact verticil of metulae and crowded sterigmata borne upon the main stem and upon one or more lateral branches that arise from the next lower node, but remain closely appressed against the main stem as illustrated in fig. 106. Branching within the penicillus is often irregular, and differentiation between the metulae and the branches or sub-branches which support these is often difficult to establish. Occasionally the structure may branch and rebranch at 3 or 4 levels below the sterigmata in at least a portion of the penicillus. On the other hand, in most members of the series, a considerable proportion of the penicilli are unbranched and show only a single terminal cluster of metulae bearing crowded sterigmata, and in some strains this type of penicillus occurs almost to the exclusion of the more complexly branched structures (fig. 108). In most members of the series the larger and more characteristic penicilli are typically borne upon conidiophores arising from the substratum, whereas the smaller and less characteristic structures are commonly borne upon aerial hyphae. In all forms the sterigmata are closely compacted at the base and may either diverge at their apices or remain essentially parallel. Conidial chains arising from the same penicillus are often of variable length and usually appear loosely parallel or divergent. There is little or no tendency toward column formation, and in age the conidial chains characteristically form a tangled mass (fig. 106). Viewed under low power, the typical penicillus is in every sense a compact brush-like structure (fig. 107E), hence the appropriateness of Dierckx's name *Penicillium brevi-compactum.*

Members of the series characteristically show stolon-like aerial hyphae which extend beyond the growing margin and return to the substratum (fig. 107F), especially when cultivated under very humid conditions, or upon especially moist substrata. In his original strain, Thom supposed this character to be diagnostic, hence applied the name *Penicillium stoloniferum* (1910) to a form which exhibited this tendency in striking manner. Subsequently it was recognized that the development of stolon-like hyphae represented a group characteristic rather than a specific one since it occurs in almost all members of the series. The structure of the penicillus appears to be a much more stable character than stolon production, which was originally thought to be significant. In the meantime, the prior but inadequate description of one of these forms by Dierckx (1901) under the exceedingly descriptive binomial, *Penicillium brevi-compactum*, came to Thom's attention. In recognition of this fact, Thom (1930) subsequently applied the designation "The Brevi-Compacta" to the series represented by

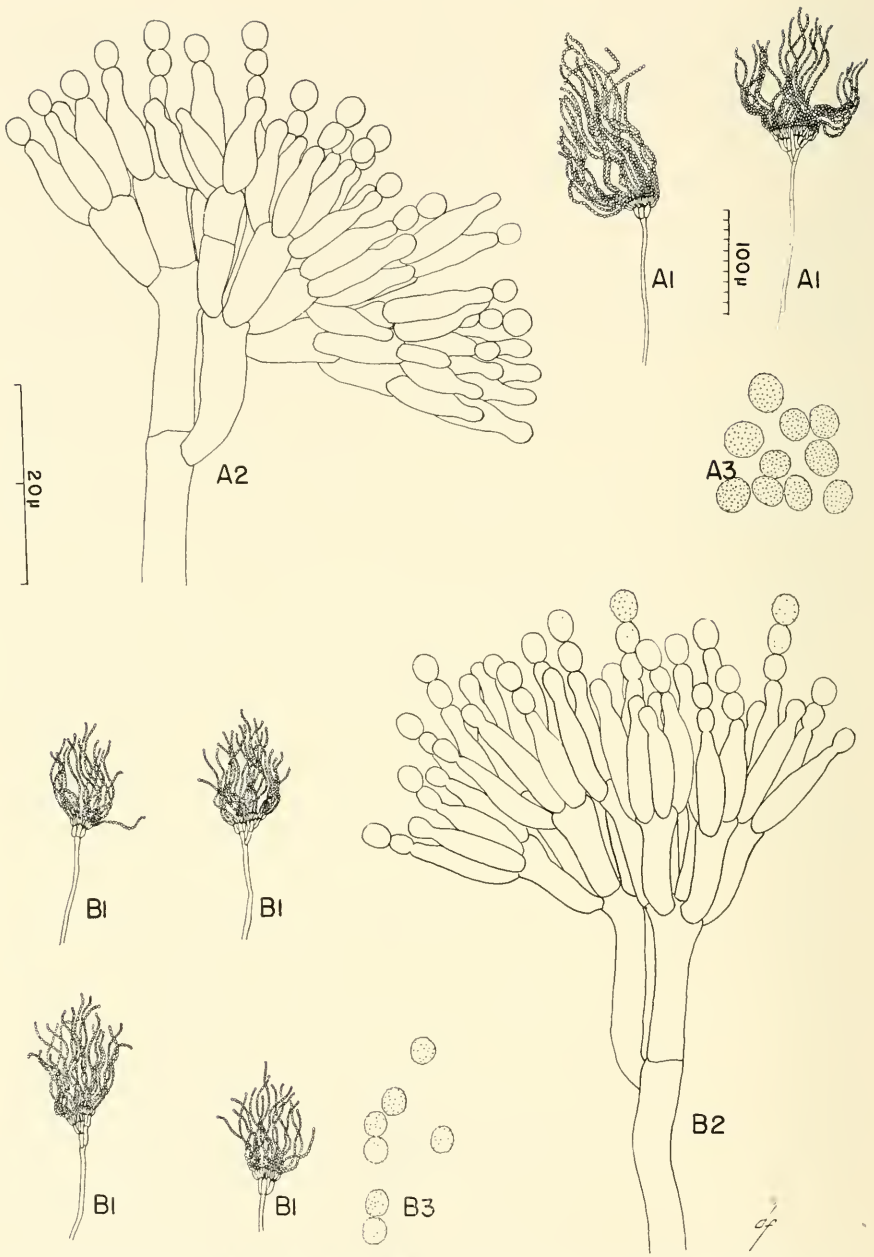


FIG. 106. *Penicillium brevi-compactum* series. A_1 and A_2, Habit sketches and detailed drawing, respectively, of typical penicilli in *P. brevi-compactum* Dierckx; A_3, Mature conidia of the same species. B_1 and B_2, Habit sketches and detailed drawing, respectively, of *P. stoloniferum* Thom; B_3, Mature conidia. This series is characterized by its very compact penicilli bearing tangled conidial chains.

P. stoloniferum and included in it numerous additional species with similar conidial structures more recently described by Biourge (1923) and Zaleski (1927).

Our current study of this series has centered upon the comparative cultural and microscopical examination of a large number of strains, including many type cultures either maintained in our Collection, or contributed by Prof. Westerdijk from the Centraalbureau in Baarn, or by Mr. George Smith of the London School of Hygiene and Tropical Medicine. These cultures appear to be quite variable, for in a number of cases cultures supposedly from the same original source now show marked differences in cultural appearance and to a lesser degree in details of microscopy. Furthermore, original descriptions of strains belonging to the series were often drawn in almost identical terms, and types received as representative of them fail to show sufficient basis for continued recognition of the species based upon them. It is thus quite impossible to differentiate between all of the species described and formerly assigned to this series. We believe that a satisfactory separation into three species can be made.

The species so accepted were among the first described, and in two of the three cases are believed to represent those most generally recognized, namely: *Penicillium brevi-compactum* Dierckx, *P. stoloniferum* Thom, and *P. paxilli* Bainier.

The first of these, for which the series is named, is characterized by its deep, looser-textured, and lightly wrinkled colonies; coarse, erect conidiophores with walls smooth or definitely roughened; and compact, often complexly branched, penicilli with cellular elements (particularly branches and metulae) commonly swollen or inflated.

The second species is characterized particularly by its restricted growth, close-texture, and strongly wrinkled colonies; comparatively thin, somewhat sinuous, smooth-walled conidiophores; and compressed and often complexly branched penicilli without marked inflation of cellular elements.

The third species is characterized by loose-textured, almost lanose colonies that are seldom strongly wrinkled, and more particularly by conidial structures usually consisting of a simple and often large terminal verticil of metulae bearing crowded sterigmata and divergent chains of conidia. Viewed under high magnification, penicilli may be strongly suggestive of *Penicillium citrinum* and allied forms except for their compactness, somewhat larger size, and slightly roughened conidiophores; viewed under low magnifications, they show masses of tangled or divergent chains of conidia rather than well marked columns.

Penicillium brevi-compactum Dierckx, in Soc. Scien. Brux. **25:** 88. 1901; Biourge, Monogr., La Cellule **33:** fasc. 1, pp. 155–157; Col. Pl. II and Pl. III, fig. 16. 1923; Thom, The Penicillia, pp. 295–296. 1930

Colonies on Czapek's solution agar growing very restrictedly, attaining a diameter of 1.5 to 2.0 cm. in 2 weeks at room temperature (fig. 107A), heavily sporing, velvety to almost lanose, loose-textured, about 1 mm. deep, often raised in central colony area, with marginal zone comparatively thin, sometimes radially furrowed, azonate or narrowly zonate, in older colonies commonly producing a yellowish zone of submerged growth extending 1–2 mm. beyond the margin of conidial development; aerial stolons occasionally seen, comparatively short and stout; growing colonies with narrow marginal zone white to cream in color, quickly shading to dull yellow-green near tea green or vetiver green in conidial areas, approaching andover green in age (Ridgway, Pl. XLVII) or in some strains deeper yellow-green; limited exudate produced mostly as small partially submerged droplets, dull yellow to deep orange-brown in color; odor slight, not distinctive; reverse in dull olive green to drab shades; conidial structures very abundant, borne in a close stand, arising primarily from a basal mycelial felt at the agar surface; conidiophores erect, usually straight and appearing more or less rigid, mostly 300 to 500μ in length, occasionally up to 700μ by 4.0 to 5.0μ with terminal area commonly swollen, conspicuously septate, with walls comparatively heavy, smooth, or delicately roughened; penicilli compact, irregularly branched with 1, 2, or more branches closely appressed, bearing crowded clusters of metulae and sterigmata and tangled conidial chains forming a loose, irregular mass 50 to 75μ in length (fig. 106A_1); branches mostly 10 to 17μ by 4.0 to 4.5μ, but commonly up to 6.5 to 7.0μ in diameter; metulae in groups of 3–6, enlarging upward, commonly wedge-shaped, measuring 9 to 12μ in length by 4.0 to 4.5μ in diameter in a median plane, commonly inflated measuring up to 6.0 to 7.0μ in diameter (fig. 106A_2); sterigmata usually 7.0 to 10.0μ by 3.0 to 3.5μ but often more or less inflated and occasionally measuring up to 5.0 to 5.5μ in diameter; conidia globose to subglobose, variable, ranging from 3.0 to 4.5μ, mostly 3.5 to 4.0μ in diameter, with walls slightly roughened.

Colonies on steep agar restricted but growing somewhat more rapidly than on Czapek, heavily sporing, about 1 mm. deep, essentially velvety and marked by numerous shallow radial furrows; limited exudate, light yellow-brown in color; penicilli essentially as on Czapek.

Colonies on malt agar like the preceding, but with radial furrows less strongly developed (fig. 107B), with marginal area more or less crenulate in old cultures from the irregular development and proliferation of stolons; penicilli as above but with conidiophore walls often more definitely roughened.

Species description based primarily upon culture NRRL 2011, received from the Centraalbureau under this name in February 1946. The strain had been received by them from Biourge in 1929 as Dierckx's species. It

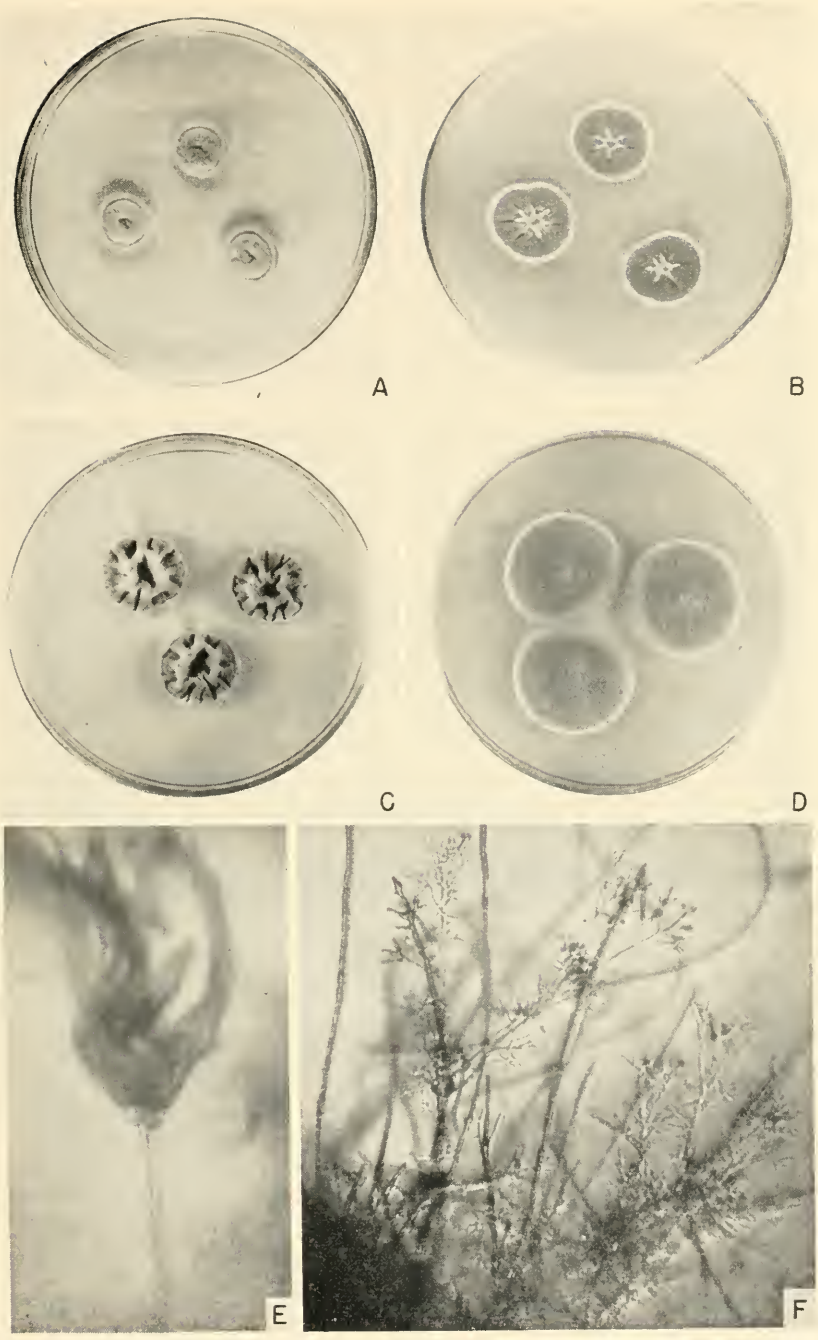


FIG. 107. *Penicillium brevi-compactum* series. *A* and *B*, Two-week old colonies of *P. brevi-compactum* Dierckx, NRRL 862, on Czapek and malt agars. *C* and *D*, *P. stoloniferum* Thom, NRRL 859, on same substrates, same age. *E*, Single penicillus of *P. brevi-compactum* as seen under high-dry objective, × 300. *F*, Colony margins of *P. stoloniferum* showing characteristic extension of growth by stolons, × 140.

is duplicated in our Collection by NRRL 862. The two cultures around which we center the above emended description of *Penicillium brevi-compactum* are distinctive, and from our current study of the *P. brevi-compactum* series, it is apparent that they do not represent *P. stoloniferum* in the sense of culture NRRL 859, which is Thom's type (Thom No. 27) of the latter species. They differ from the more widely distributed *P. stoloniferum* in showing (1) more restricted colonies, (2) coarser and larger conidiophores, and (3) branches, metulae, and sometimes sterigmata that are definitely inflated. Two strains received from the Centraalbureau in February 1946 as *P. hagemi* Zaleski (their isolations) produce colonies of deeper yellow-green colors but show the same general colony characteristics as noted above, and usually produce penicilli with cellular elements inflated. These cultures, now maintained as NRRL 2012 and 2013, are regarded as representing hardly more than normal variations within the species *P. brevi-compactum* Dierckx.

A culture brought by Dr. Simonart in 1936 from the Biourge collection as *Penicillium brevi-compactum* Dierckx (Biourge's No. 42) and now maintained as NRRL 863, shows a fairly compact penicillus suggestive of the present series but produces colonies in much darker green shades, conspicuously roughened conidiophores, and a strong penetrating earthy odor. These latter characters are believed to indicate relationship to the *P. terrestre* series. If the culture can be considered in the *P. brevi-compactum* series at all, it must be regarded as transitional toward *P. terrestre* Jensen and *P. solitum* Westling (see pp. 450–455).

A number of described species are believed to approximate *Penicillium brevi-compactum* Dierckx as presented above. Undoubtedly these were based upon strains believed to possess distinctive characters. When original descriptions and figures are compared, and type strains still in existence are examined in parallel cultures, the bases for species separations largely disappear. Among species believed to be inseparable from *P. brevi-compactum* Dierckx are included the following:

Penicillium crassum Sopp (Monogr., p. 147–148, Taf. XVI, fig. 111; Taf. XXII, fig. 15. 1912; Thom, The Penicillia, pp. 297–298. 1930) is known only from the author's original description. The species was apparently based upon some member of the *P. brevi-compactum* series but closer identification is now impossible; bodies suggesting sclerotia were reported as occasionally produced on rice. Insofar as we know, this is the only report of sclerotia being produced by a member of the series.

Penicillium bialowiezense Zaleski (in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 450–451, Taf. 39. 1927; Thom, The Penicillia, pp. 303–304. 1930) was described as producing thin, plane, velvety colonies with central areas sometimes convex, bearing conidiophores 400 to 600μ by 4.0 to 5.0μ, with penicilli comparatively long

but described and figured as clearly belonging in this series, and showing delicately roughened walls; conidia ovate to subglobose, 2.5 to 3.5μ in long axis. Thom's notes (1930) made on a culture received from Baarn as Zaleski's type describe colonies of the general type reported by Zaleski, and likewise describe conidiophore walls as pitted or granular; conidia were observed by him to be elliptical and to range from 3.0 to 3.5μ in long axis. A culture received from Baarn under this name in 1946 produces colonies indistinguishable from *P. stoloniferum*. The species obviously represents some member of the *P. brevi-compactum* series, and basing our opinion upon original descriptions rather than cultures now in our possession, *P. bialowiezense* is regarded as probably approximating *P. brevi-compactum* Dierckx.

Penicillium hagemi Zaleski (in Bul. Acad. Polonaise Sci.: Math. et. Nat. Ser. B, pp. 448–450; Taf. 39. 1927. Thom, The Penicillia, pp. 298–299. 1930) was described with colonies growing restrictedly, radiately wrinkled and centers elevated with conidiophores from 300 to 400μ by 3.5 to 4.0μ, either smooth or rough walled; the penicillus was reported and figured as showing 2 or 3 comparatively long branches with walls occasionally roughened; metulae and sterigmata fairly compactly arranged; conidia ovate to subglobose, 2.5 to 3.5μ in diameter. Thom's notes (1930) made from the type strain confirmed the above in general but failed to mention the character of the conidiophore walls. The species is believed to be inseparable from *P. brevi-compactum* as described above. A culture received from George Smith under this name as a culture from Baarn (and probably type) shows penicilli with cellular elements and conidia large but otherwise representative of the series. Two cultures received from Baarn as their isolates of *P. hagemi* present well enough the characteristics attributed to the species by Zaleski, but fail to show sufficient differences to warrant recognition as a separate species in the *P. brevi-compactum* series.

Penicillium patris-mei Zaleski (in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 496–498, Taf. 58. 1927; Thom, The Penicillia, p. 303. 1930) was described as producing strongly wrinkled, irregular colonies with conidiophores extremely variable in length and 2.0 to 2.5μ in diameter, commonly flexuous with walls smooth and bearing compact asymmetric penicilli. Thom's notes (1930) made on a strain from Baarn as Zaleski's type described buckled and radiately wrinkled colonies with yellowish green conidial areas and reverse in yellowish to grayish brown; penicilli were reported to be of the *P. brevi-compactum* type with metulae compacted at the base, bearing crowded sterigmata and conidia more or less elliptical, about 3.5μ in long axis. Cultures received under this name from George Smith and Baarn, and believed to have stemmed from Zaleski's type, show conidiophores sometimes roughened, and clearly belong with *P. brevi-compactum* Dierckx as described above.

Penicillium szaferi Zaleski (in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 447–448, Taf. 38. 1927; Thom, The Penicillia, pp. 299–300. 1930) was described as producing restricted, radiately wrinkled colonies with surface hirsute, pale green to dark yellow-green in color; conidiophores 300 to 500μ by 4.0 to 4.5μ, with walls slightly asperulate; penicilli were comparatively large with metulae and sterigmata arranged compactly. Thom's notes (1930) made from the type indicated colonies of the same general pattern, but reported conidiophores smooth-walled. No authentic cultures have been available for the present study but the species is regarded as probably inseparable from *P. brevi-compactum* Dierckx, as presented above.

Penicillium stoloniferum Thom, in U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, 68–69, fig. 26. 1910. Thom, The Penicillia, pp. 292–294, figs. 41 and 42. 1930

Colonies on Czapek's solution agar (Col. Pl. VI) growing restrictedly, attaining a diameter of 2.0 to 2.5 cm. in 12 to 14 days at room temperature, strongly wrinkled and buckled in most strains (fig. 107C), with central areas often conspicuously raised and in age often splitting through the underlying agar, typically consisting of a close-textured mycelial felt bearing abundant conidial structures, with surface velvety to lanose in most strains but more or less floccose in others, usually azonate when young but commonly becoming narrowly zonate in age; conidial structures abundantly produced throughout the whole colony but generally in greater abundance in marginal to submarginal areas, typically in yellow-green shades approximating gnaphalium green to light celandine green (Ridgway, Pl. XLVII) when young to sage green or artemisia green (R., Pl. XLVII) in mature fruiting areas, and approaching stone gray (R., Pl. LII) in age; limited clear to pale yellow exudate produced in some strains, not in others; odor neither pronounced nor distinctive; reverse dull yellow to gray or greenish gray, with surrounding agar uncolored or lightly tinted in the same shades; colony margins usually entire and compact during the growing period but characterized by the presence of stolon-like aerial hyphae which re-enter the substratum beyond the limits of the submerged vegetative mycelium (fig. 107F). This development is especially pronounced in young colonies on "wet" agar. Penicilli typically short and compact with constituent elements closely appressed, bearing parallel or divergent chains of conidia (fig. $106B_1$), and withal presenting the picture of a short, compact brush; conidiophores arising either from the substratum, or as lateral branches from aerial hyphae, the former ranging up to 250μ in length by 3.5 to 4.0μ in diameter, the latter from 35 to 100μ by 3.0 to 3.5μ, larger penicilli typically consisting of the main axis bearing a verticil of metulae and closely compacted sterigmata and one, or occasionally more, side branches each terminated by like spore bearing elements (fig. $106B_2$), smaller penicilli commonly show only a single terminal verticil of metulae surmounted by crowded sterigmata; branches usually 10 to 25μ by 3.0 to 3.5μ, with subbranches occasionally evident; metulae parallel or slightly divergent, ranging from 3 to 6 in number and varying from 8 to 12μ by 2.8 to 3.8μ; sterigmata borne in compact clusters of 4 to 8, not distinctive in form, with spore bearing tubes comparatively short, generally measuring 8 to 10μ by 2.2 to 2.8μ; conidia elliptical when young but becoming globose to subglobose at maturity, sometimes pyriform, finely roughened, usually 2.5 to 3.5μ in diameter.

Colonies upon steep agar attaining a diameter of 3.5 to 4.0 cm. in 12 to 14 days at room temperature, but usually similar to the above in basic pattern and coloration, sometimes narrowly zonate, often heavier sporing; microscopic details of penicilli as described above.

Colonies upon malt extract agar attaining a diameter of 3.0 to 3.5 cm. in 12 to 14 days at room temperature, plane, velvety (fig. 107D), often becoming more or less zonate in marginal areas after 12 to 14 days; details of microscopic structure as above.

Species descr ption based primarily upon the following strains: The type, NRRL 859 (Thom No. 27), isolated by Thom from a rotting mushroom in the summer of 1904 at Storrs, Connecticut, and maintained continuously in culture since that time without apparent change in colony appearance or details of structure; NRRL 860 (Thom No. 79) isolated by Thom in 1908 from maple sugar at Storrs; three cultures received from the Centraalbureau under this name in May 1946; a strain received from the same source as *Penicillium biourgeianum* Zaleski (see below) and numerous other strains examined during the current study and in previous years.

Marked variation is regularly encountered among strains regarded by us as representing *Penicillium stoloniferum* Thom. Other workers have considered individual isolates sufficiently distinctive to warrant species status, and have so described them under other names. However, when large numbers of strains are examined in parallel cultures, as in the present work, many of the assumed distinctions disappear and the validity of these species becomes questionable. Described species that are believed to approximate *P. stoloniferum* Thom include the following:

Penicillium griseo-brunneum Dierckx (Soc. Scien. Brux. **25:** 88. 1901. In Biourge Monogr., La Cellule **33:** fasc. 1, pp. 162–163; Col. Pl. II and Pl. III, fig. 19. 1923; Thom, The Penicillia, p. 302. 1930) was reported by Biourge in terms which indicated close relationship to *P. stoloniferum* Thom. Thom's culture notes (1930) on a strain presumed to be type, failed to show differences adequate to separate Dierckx's species from *P. stoloniferum*. Strains received from the Centraalbureau and from George Smith under this name and included in the present study, differ from the type of *P. stoloniferum* only in producing somewhat faster growing colonies with marginal areas on Czapek's agar thin and somewhat submerged.

Penicillium erectum Bainier, (Bul. Soc. Mycol. France **23:** 13, Pl. III, figs. 1–16. 1907; Thom, The Penicillia, p. 295. 1930) is known only from the author's original description. Conidiophores were reported as long, unbranched, about 5.6μ in diameter and to bear penicilli with one or two series of branches in 1-sided verticils surmounted by verticils of metulae and sterigmata. The description and figures indicate some member of the *P. brevi-compactum* series, probably approximating *P. stoloniferum* Thom.

Penicillium tabascens Westling (Arkiv för Botanik **11:** pp. 56, 100–102; figs. 20, 61. 1911; Thom, The Penicillia, pp. 300–301. 1930) as known by a culture received from

Westling under this name and discussed by Thom in 1930, closely approximated *P. stoloniferum* Thom, with which the species should be regarded as synonymous.

Penicillium biourgeianum Zaleski (in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 462–464; Taf. 45 and 48. 1927. Thom, The Penicillia, pp. 296–297. 1930) was described as producing restricted, irregular colonies with conidial areas in blue-green shades and reverse pale yellow to orange. Conidiophores were reported as from 500 to 700μ by 3.0 to 4.0μ, straight or slightly flexuous, with apices usually inflated and with all walls smooth; penicilli irregularly branched, asymmetrical with metulae fairly long 12 to 16μ by 2.5 to 3.5μ and showing inflated apices; conidia smooth, globose 2.5 to 3.0μ in diameter. Thom's notes (1930) on the type strain described a restricted, radiately wrinkled colony with surface velvety, bluish green to green in color becoming olive green or gray-green in age; conidiophores 100 to 200μ by 2.0 to 3.0μ with apices inflated; penicilli consisting of a single verticil of metulae, or with one branch, and with metulae and sterigmata closely packed at the base. The species was assigned to the *P. brevi-compactum* series with his *P. stoloniferum*. Re-examination of type cultures from the Centraalbureau and from George Smith in our current study show a form indistinguishable from *P. stoloniferum* Thom except for conidial areas in somewhat darker dull green shades.

Penicillium paxilli Bainier, in Bul. Soc. Mycol. France **23:** 95–96; Pl. X, figs. 1–4. 1907. Thom, The Penicillia, pp. 294–296. 1930

Colonies on Czapek's solution agar attaining a diameter of 3.0 to 4.0 cm. in 10 days to 2 weeks at room temperature, plane or showing a limited number of shallow radial furrows (fig. 108A), heavily sporing throughout, velvety in younger conidial areas with central portion of colonies commonly showing an overgrowth of vegetative mycelium from which secondary conidial structures are developed, growing margins about 1 mm. in width, white, succeeded by a narrow zone of young fruiting structures approximately artemisia green (Ridgway, Pl. XLVII) but shading quickly to darker olive green shades near andover green (R., Pl. XLVII); exudate abundant, produced as small droplets largely embedded in the mass of upright conidiophores, commonly showing a cup-like or nodular arrangement of secondary conidial structures surrounding the droplets in older colony areas; odor "moldy", not pronounced; reverse in dull yellow to cinnamon drab shades; conidiophores borne in a dense stand arising primarily from the substratum, occasionally as branches from aerial hyphae, variable in length but commonly 150 to 200μ by 3.5 to 4.0μ, sometimes longer, with walls slightly roughened; penicilli compact, 20 to 25μ in length, consisting of a single terminal verticil of 5 to 8, or 9 metulae from which arise divergent chains and loose columns of conidia up to 100 to 150μ in length; metulae 10 to 12μ by 2.8 to 3.3μ, uniform in diameter or with apices only slightly enlarged; sterigmata 8 to 10μ by 2.0 to 2.5μ; conidia elliptical to subglobose, 2.8 to 3.3μ in long axis, with walls thin, smooth or nearly so.

Colonies on steep agar growing somewhat more rapidly than on Czapek,

4.0 to 5.0 cm. in 2 weeks at room temperature, in texture and color essentially duplicating the above; penicilli similar in pattern to the above but commonly showing loose masses of conidial chains up to 200μ in length.

Colonies on malt agar 5.0 to 6.0 cm. in 2 weeks at room temperature,

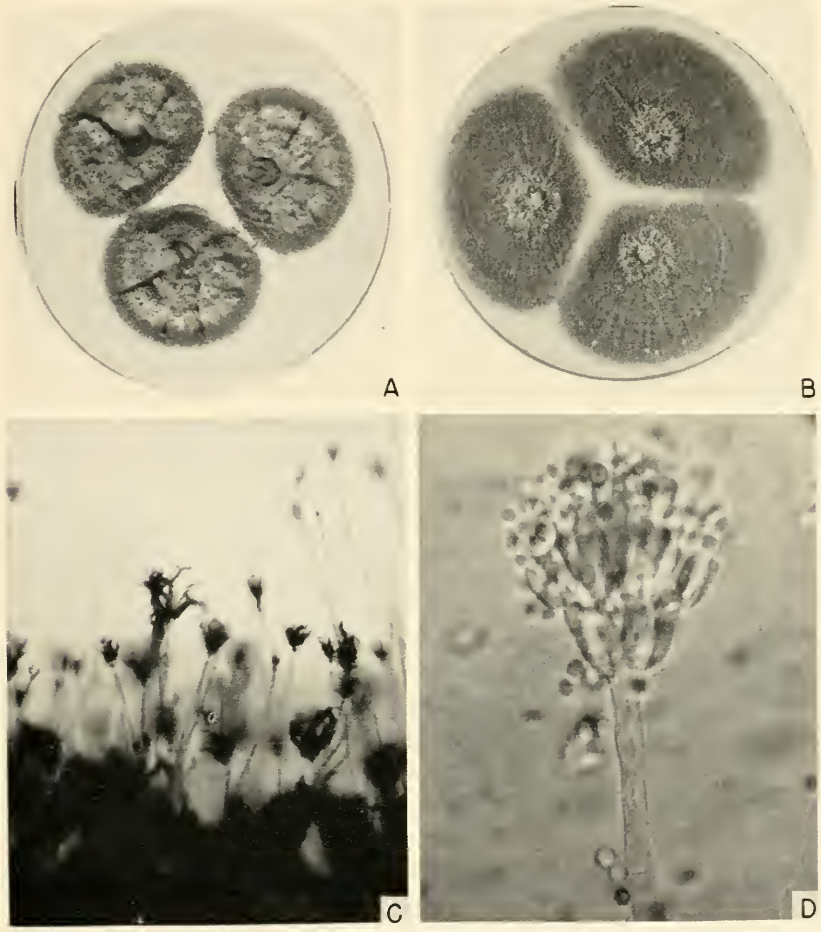


FIG. 108. *Penicillium paxilli* Bainier, NRRL 2008. *A* and *B*, Two-week old colonies on Czapek and malt agars. *C*, Colony margin showing characteristic aspect of penicilli as seen under low-power, × 90. *D*, Detail of single penicillus, × 1100.

plane, essentially velvety or with limited aerial overgrowth in colony center, more or less zonate, in dull yellow-green shades near grayish olive; penicilli as on the preceeding medium.

Bainier described *Penicillium paxilli* as a dark bluish green form with

comparatively long conidiophores, 1 mm. in length, bearing compact penicilli consisting typically of a terminal verticil of 4–8 metulae. In the present study numerous strains have been observed which, in general, comply with this description except that the conidiophores are generally shorter. Representative of this species is strain NRRL 2008 received from Prof. W. H. Weston as a culture isolated from optical instruments by Prof. W. G. Hutchinson, Barro Colorado Island, Panama. Forms of this type were not uncommon among the cultures isolated from deteriorating military equipment.

The presence of a terminal verticil of metulae is strongly suggestive of the *Penicillium citrinum* series. Typical strains of *P. paxilli* as considered here, however, differ from *P. citrinum* in the following particulars: (1) penicilli are consistently larger, *i.e.*, composed of a large number of elements, and are more compact; (2) colonies are looser in texture and conidiophores are coarser, more consistently erect, and are finely roughened; (3) the colony colors are in darker shades, quickly becoming dull dark green near andover green (R., Pl. XLVII) in contrast to the lighter blue-green colors of the *P. citrinum* series which approximate artemisia to lily green (R., Pl. XLVII); and (4) representatives of this species do not produce citrinin. *Penicillium paxilli*, as understood by us, also bears resemblance to *P. raistrickii* Smith. It differs from the latter species, however, in producing a greater number of metulae which are more compactly arranged and in its failure to develop sclerotia upon any substratum tested.

Occurrence and Significance

Members of the *Penicillium brevi-compactum* series are apparently widely distributed but not particularly abundant in nature. As previously noted, strains are not infrequently isolated from soil, from decaying fleshy fungi, and from slowly decomposing vegetable products, including cereal grains.

Alsberg and Black (1913) isolated a strain of *Penicillium stoloniferum* from moldy Italian maize and obtained from it a new metabolic product, mycophenolic acid, with the empirical formula $C_{17}H_{20}O_6$, deduced from analysis, titration value, and estimated molecular weight. It crystallized as white needles, melted at 140°C., and gave a violet color with $FeCl_3$ in aqueous solution. J. H. V. Charles (in Clutterbuck, *et al.*, 1932), twenty years later, isolated additional strains from similar material. Grabe (1942) reported *P. stoloniferum* to represent one of the molds commonly developing in bread. The infection could easily be carried in from the field.

The biochemistry of the *Penicillium brevi-compactum* series has been carefully investigated by Professor Raistrick and his associates. Clutterbuck, Oxford, Raistrick, and Smith (1932) reported 14 out of the 15 strains tested to produce a mixture of phenolic acids, *viz.* mycophenolic acid

($C_{17}H_{20}O_6$) and four additional metabolic products having the following empirical formulae: $C_8H_6O_6$, $C_{10}H_{10}O_5$, $C_{10}H_{10}O_6$, and $C_{10}H_{10}O_7$. The last two acids were present in every instance; whereas $C_8H_6O_6$ and $C_{10}H_{10}O_5$ were probably formed but were not detectable with certainty in all cases because of the small yields. Mycophenolic acid, having the largest molecule, was formed by only 12 strains. It was noted that freshly isolated strains gave the highest yields of mycophenolic acid while those long maintained in culture tended to lose the capacity to produce this product while retaining their ability to produce the smaller molecules. None of the phenolic acids were produced by a strain of *P. aurantio-griseum* Dierckx var. *poznaniensis* Zaleski, which Thom, because of the compact character of its penicilli, had assigned to the *P. brevi-compactum* series in 1930 (see p. 496). Oxford and Raistrick (1932), investigating the product $C_8H_6O_6$, reported it to be 3:5-dihydroxyphthalic acid (M.P. 188–190°C.) and hence constitutionally related to a large group of lichen acids. In the following year, the same investigators (1933a) elucidated the molecular constitution of the products $C_{10}H_{10}O_5$, $C_{10}H_{10}O_6$, and $C_{10}H_{10}O_7$, and reported these acids to be closely related to each other, to 3:5-dihydroxyphthalic acid and to mycophenolic acid, and to divaricatic acid from lichens. The molecular constitution of mycophenolic acid was considered in an accompanying paper by Clutterbuck and Raistrick (1933). In a fifth paper Oxford and Raistrick (1933c) investigated the production of the different phenolic acids by a strain of *P. brevi-compactum*. The yield of mycophenolic acid increased throughout the incubation period of 56 days, although 50 per cent of the total was present at 8 days. $C_{10}H_{10}O_7$ could not be detected in early stages and 40 per cent of the total appeared after the glucose was used up. $C_{10}H_{10}O_6$ increased rapidly to a maximum in 15 days, after which it declined to zero at 56 days. $C_8H_6O_6$, never present in large amounts, increased steadily throughout the whole period, 60 per cent being formed after the glucose was consumed. Finally, $C_{10}H_{10}O_5$ was present in very small amounts in the early stages of metabolism but absent after 22 days. No satisfactory explanation covering the initial steps in their formation from glucose was evolved.

Investigating the mycelial constituents of *Penicillium brevi-compactum* and related species, Oxford and Raistrick (1933b) isolated ergosteryl palmitate from all but one of 15 strains investigated. In most cases the yield of recrystallized ergosteryl palmitate was of the order of 0.02 per cent of the dry weight of the mycelium. In a single instance, *viz.*, *P. aurantio-griseum* Dierckx var. *poznaniensis* Zaleski (Cat. No. P69), the yield of purified ester was as high as 0.5 per cent. This strain, it will be recalled, had failed to produce the phenolic acids characteristic of other members of the series (Clutterbuck, *et al.*, 1932). The biochemical behavior of this mold be-

comes of special interest and significance when one considers the true identity of the strain in question. Three cultures in our possession purported to represent Zaleski's variety, and all presumably derived from his type, when examined in our current study uniformly represented some member of the Fasciculata approximating *P. cyclopium* West., hence are not closely related to the *P. brevi-compactum* series. Oxford and Raistrick also noted a yield of 0.4 per cent ergosteryl palmitate from the mycelium of a strain of *P. italicum*. This too is interesting, for Zaleski's variety is more nearly related to this species than to the *P. brevi-compactum* series.

Wilkins and Harris (1943) reported a strain of *Penicillium brevi-compactum* to produce an antibiotic that inhibited the growth of *Staphylococcus aureus*, but not *Escherichia coli* or *Pseudomonas aeruginosa*. Florey, *et al.* (1946) subsequently demonstrated that this antibiotic action was due to mycophenolic acid and investigated, in limited detail, methods for its production and recovery. It was shown to be comparatively active against species of *Corynebacterium* and to inhibit the growth of some pathogenic fungi. Abraham (1945) reported culture liquors from *P. brevi-compactum* to contain normycophenolic acid ($C_{16}H_{18}O_6$) which acted as a growth inhibitor for *S. aureus*. The compound had been previously noted by Clutterbuck and Raistrick (1933).

Oxford and Raistrick (1935) reported the production of *i*-erythritol in small yields from the mycelia of *Penicillium brevi-compactum* and *P. cyclopium* Westling (see p. 507).

Chapter X

ASYMMETRICA

Sub-section: LANATA

In this section of the Asymmetrica, colonies show an aerial vegetative mycelium consisting of a cottony, lanose or floccose mass, web or felt. Conidiophores generally arise as branches from the aerial mycelium, less commonly directly from the substratum. Conidial areas commonly appear centrally after the establishment of the definite aerial felt and progress toward the marginal areas. In some species the characteristic aerial felt diminishes toward the end of the growing period, leaving the margin velvety. Penicilli are usually comparatively large and irregularly branched, with metulae and sterigmata often arising at different levels in the fruiting structure. Conidiophores are, as a rule, fairly coarse with walls more or less roughened. Conidial chains usually form tangled rather than columnar masses.

Following Thom's Monograph (1930), we have included a number of species in the Lanata which Biourge placed in his Zonata, since we believe that the floccose aerial felt as a character brings together more nearly related species than the formation of zones in the colonies as Biourge grew them.

The lines used to separate the Lanata are admittedly arbitrary. In fact the section merges insensibly into each of the other sections of the Asymmetrica, and forms are placed in one or the other upon the judgment of the observer as to where they may be most easily identified. Species that may be strongly floccose but which produce definitely divaricate fruiting structures are placed in the Divaricata. Species which may produce more or less flocculent colonies but which present an overall velvety effect and which are unmistakably closely related to strictly velvety species are included in the Velutina. Species predominantly floccose, and with penicilli of the same general type as the Lanata, but showing trailing or ascending bundles of hyphae are assigned to the Funiculosa. Species in which conidiophores arise primarily from the substratum and collect into definite tufts or bundles are automatically placed in the Fasciculata.

The lines of demarcation between the Lanata and the Fasciculata, in particular, are often difficult to establish; and there are reasons for believing that the entire *Penicillium commune* series, with the possible exception of *P. lanosum* West. (see p. 431), represents an assemblage of forms in which fasciculation is lacking but which are morphologically and

physiologically closely related to definitely fasciculate species. Abandonment of the Lanata section has been considered on this account. It is retained, however, since we feel that the user of the Manual will, through it, experience less difficulty in locating certain well-defined and long-recognized species than through any other approach now available. The user of this Manual should, however, guard against assuming that the Lanata, except for the *P. camemberti* series, represents a natural grouping of strains that should be expected to exhibit unique biochemical or physiological characteristics.

Key to the Lanata

I. Colonies typically floccose, without evidence of fascicles or ropes of hyphae, or with such structures reduced and inconspicuous if present.

A. Colonies predominantly white, remaining so, with the development of ripe conidia or becoming lightly colored in gray-green shades.
P. camemberti series 421

1. Colonies remaining white indefinitely ..... *P. caseicolum* Bainier 422
2. Colonies with surface becoming pale gray-green or greenish glaucous within 10 to 14 days ..... *P. camemberti* Thom 426

B. Colonies quickly developing some shade of green in conidial areas.
P. commune series 429

1. Vegetative mycelium uncolored and with reverse uncolored or in drab shades, usually heavily sporing on malt agar.
a. Conidia globose or nearly so, less than 4.0μ in diameter, finely roughened ..... *P. lanosum* Westling 431
b. Conidia elliptical or in age becoming subglobose, commonly up to 4.0μ or more in diameter, smooth-walled.
1′. Conidial areas in rather bright yellow-green shades.
P. lanoso-viride Thom 434
2′. Conidial areas bluish green to gray-green.
aa. Conidial areas with blue element pronounced, near bluish glaucous, deeply floccose ..... *P. lanoso-coeruleum* Thom 436
3′. Conidial areas with green to gray-green shades predominating; at first court gray to gnaphalium green, becoming olive in age.
aa. Colonies with unusually strong actinomyces-like odor.
P. biforme Thom 437
bb. Colonies with odor less pronounced.
1″. Colonies forming a felt 300 to 1000μ deep.
P. commune Thom 439
2″. Colonies deeply floccose, 1 to 2 mm. deep.
P. lanoso-griseum Thom 441

2. Vegetative mycelium yellow to orange, at least adjacent to the substratum; reverse orange to bay; non-sporulating or very lightly sporulating on malt agar.
a. Colonies deep, 2.0 to 3.0 mm., loosely floccose, lightly sporulating upon Czapek and steep agars ..... *P. aurantio-candidum* Dierckx 442
b. Colonies thinner, definitely fasciculate, usually heavily sporing on Czapek and steep agars ..... *P. aurantio-virens* Biourge 503
(in *P. cyclopium* series, p. 490)

II. Colonies showing ropes of hyphae or poorly defined fascicles at the margin.
P. terrestre series 446
(in the Funiculosa, p. 445)
III. Colonies showing conidiophores aggregated into definite tufts or fascicles.
The Fasciculata 467

Penicillium camemberti Series

(Camembert-type cheese molds)

Outstanding Characters

Colonies floccose, cottony, deeply lanose, at first pure white and at maturity remaining white or becoming pale gray-green depending upon the species, reverse and agar uncolored or nearly so.

Conidiophores arising from the substratum or from the loose aerial felt, variable in length up to 500 to 600μ by 3.0 to 4.0μ in diameter, with walls more or less roughened.

Penicilli asymmetric, irregularly branched and variable in pattern, with metulae and sterigmata commonly arising at different levels, bearing conidia in tangled chains to form an irregular brush up to 100 to 150μ in length.

Conidia at first elliptical, becoming subglobose at maturity, smooth-walled, comparatively large, about 4.0 to 5.0μ in diameter.

Series Key
(See General Key to Lanata)

Members of this series regularly occur upon and are responsible for the production of soft cheeses of the Camembert type, including Camembert, Brie, and Neufchatel. Their natural habitat outside the cheese industry is not known. Strains in our possession, and those reported in the literature, have been obtained from cheese samples or from the ripening rooms where such cheeses are matured.

Whereas all members of the series appear to be closely related, two well-defined species are recognizable upon the basis of their cultural characteristics, namely: *Penicillium camemberti* Thom and *P. caseicolum* Bainier. Of these species the former is characterized by the production of pale gray-green conidia, whereas the conidia of the latter are uncolored and are almost indistinguishable from the background of floccose, white mycelium when viewed superficially. The two species likewise differ in physiological and biochemical characteristics as revealed in cheese manufacture, further emphasizing their identities as separate species. Members of the series have been widely studied because of their role in cheese manufacture. Many names have been used and species descriptions published for several of these. All of them, however, seem to fall into either one or the other

of the two species noted above, and the synonymy for the series is considered in connection with our discussions of these species.

The true relationship of *Penicillium camemberti* and *P. caseicolum* is not known. Culturally they are strikingly similar except for conidial color, and commercially they are used for the manufacture of essentially similar cheeses, although the former is more actively proteolytic and produces a somewhat softer product (fig. 111). There is a possibility that *P. caseicolum* represents a naturally produced colorless mutant of *P. camemberti* since such are known to have developed in other species, including *P. urticae*, *P. citrinum*, and *P. chrysogenum*. No proof of such origin, however, is available and there are sufficient cultural and physiological differences between the two to separate them easily—hence both are recognized.

Penicillium caseicolum Bainier, in Bul. Soc. Mycol. France **23:** 94, Pl. X, figs. 6–10. 1907. Thom, The Penicillia, pp. 310–312, fig. 44A. 1930.

Synonyms: *P. camemberti* var. *rogeri* Thom, in U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118: 52–53, fig. 17, 1910.

P. epstcinii Lindau, in Deutsch. Krypt. Flora, Pilze **8:** 166. 1904–1907.

P. rogeri Wehmer, in Lafar Tech. Mycol. 2 aufl. **4:** 226. 1906.

Colonies on Czapek's solution agar growing rather restrictedly, 2.0 to 2.5 cm. in diameter in 2 weeks at room temperature, deeply floccose, cottony, azonate (fig. 110A), central areas 2 to 3 mm. deep, white, slightly furrowed, often in quadrants, conidial heads abundant, white, borne upon long conidiophores arising from aerial hyphae or direct from the substratum; limited exudate produced as small droplets, often embedded in the mycelial mass, colorless; odor more or less definite, suggestive of potato peels; reverse colorless or nearly so; conidial structures inconspicuous from lack of color, abundantly produced over the entire colony area, particularly abundant along inter-colony margins, usually large, asymmetric but variable in form and dimensions, bearing conidial chains more or less divergent or tangled, seldom parallel and never tending to form columns (fig. 109A); conidiophores variable in length, commonly up to 400 to 450μ when arising from the substratum or 50 to 100μ when borne as branches from aerial hyphae, generally 3.0 to 4.0μ in diameter, commonly roughened (fig. 109B); penicilli ranging from 60 to 85μ in length, asymmetric, branching irregularly at 2 or 3 levels below the metulae and sterigmata (fig. 109A), bearing conidial chains up to 50 to 75μ in length; branches variable in dimensions but commonly ranging from 15 to 25 or 30μ by 3.0 to 4.0μ,

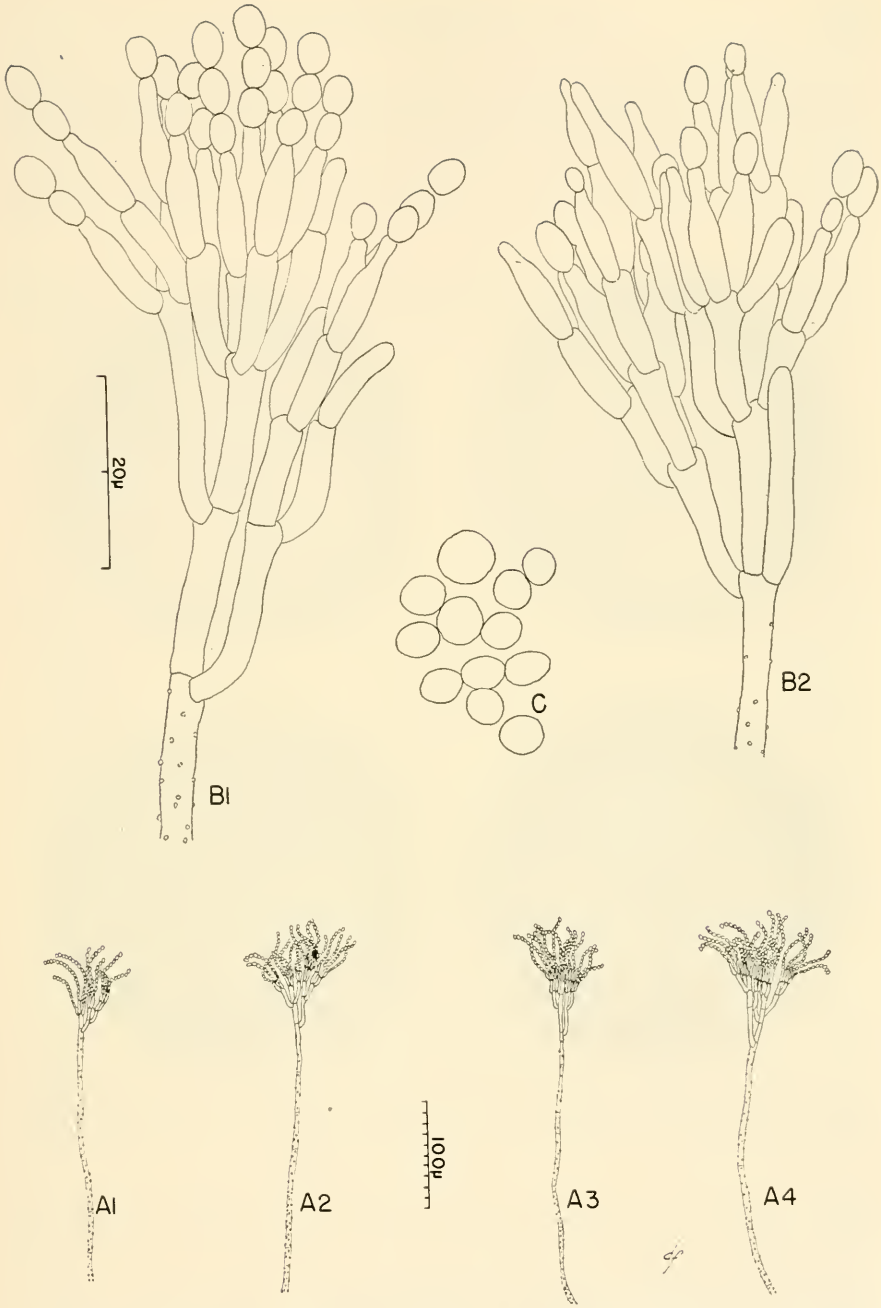


FIG. 109. *Penicillium caseicolum* Bainier. A_1–A_4, Habit sketches of representative penicilli. B_1 and B_2, Detailed drawings showing characteristic irregularity in the arrangement of cellular elements—conidiophores slightly roughened. *C*, Mature conidia.

with walls frequently roughened; metulae borne at different levels within the penicillus, usually 8.0 to 12.0μ by 2.5 to 3.0μ; sterigmata ranging from 10 to 13μ by 2.2 to 2.5μ, with metulae and sterigmata often not clearly differentiated and commonly arising at the same level, usually borne in small clusters; conidia elliptical when first formed, becoming globose or

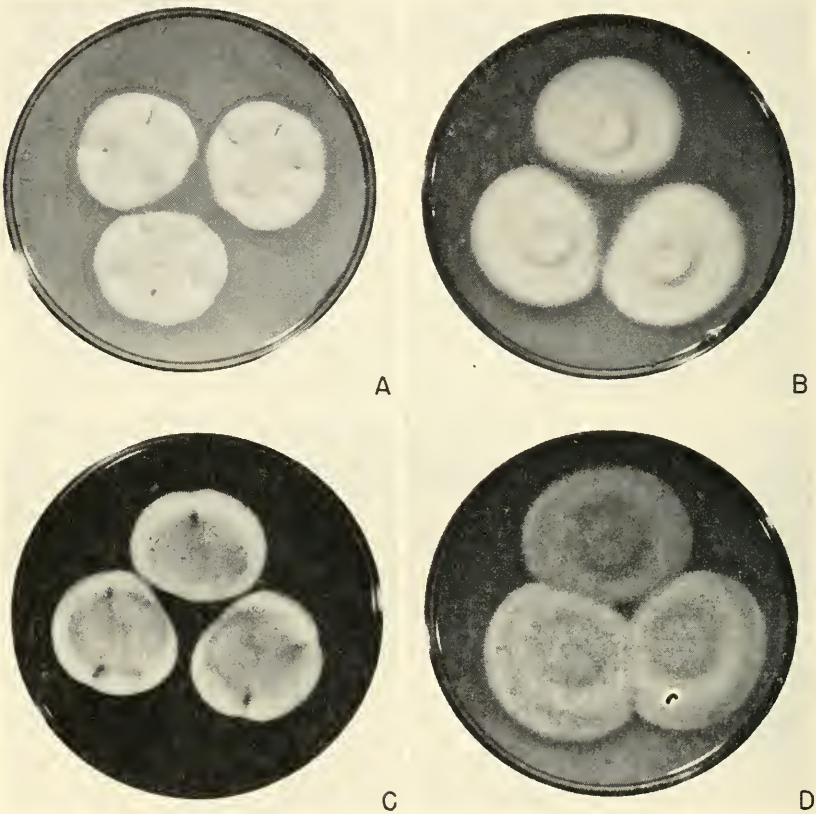


FIG. 110. *Penicillium camemberti* series. *A* and *B*, Two-week old colonies of *P. caseicolum* Bainier, NRRL 874, on Czapek and malt agars. *C* and *D*, *P. camemberti* Thom, NRRL 877, with substrata and age as in the preceding.

subglobose in age (fig. 109C), smooth-walled, ranging from 4.0 to 5.0μ by 3.3 to 4.5μ.

Colonies on steep agar, cottony, white, azonate, 2 to 3 mm. deep in central area attaining a diameter of 3.0 to 3.5 cm. in two weeks; exudate clear, abundant as droplets partially buried in the colony; sporulating

more abundantly than on Czapek and with conidiophores longer, up to 800μ in length; penicilli often larger, but otherwise as described above.

Colonies on malt agar duplicating the above but not producing exudate (fig. 110B) and with conidiophores up to 1 mm. or even longer; bearing penicilli usually about 100μ in length.

The species is characterized by its complete lack of color, the very loose and rangy character of its spore-bearing apparatus, and the tendency to branch repeatedly and to bear metulae and sterigmata at various levels.

Species description based upon NRRL 875—from the Thom Collection as No. 4640.440. This culture was received by Thom from the Bainier Collection as *Penicillium caseicolum* and may be regarded as type. A second strain, NRRL 874, obtained from the Thom Collection as No. 6, isolated by him in 1904 from Camembert cheese and used as the basis of his *P. camemberti* var. *rogeri*, duplicates NRRL 875 in all particulars. NRRL 876, from the Thom Collection as No. 4733.26 (Biourge's No. 157), clearly belongs with strains NRRL 874 and 875. It, however, is even more floccose than these strains and produces very few conidial heads on either of the three substrata generally used in this study. On Czapek's solution agar colonies show a faint wine color in central areas in reverse. NRRL 876 was received from Biourge in 1924 as *Penicillium candidum* Roger (cited by Biourge in his Monograph, La Cellule **33:** fasc. 1, 193–194; Col. Pl. III and Pl. V, fig. 27, 1923). A strain received from the Centraalbureau as Thom's *P. camemberti* var. *rogeri* Thom in February 1946 represents a typical strain of *P. caseicolum* Bainier. Thom had proposed this usage in 1910 (U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, pp. 52–54) to cover the pure white form isolated from cheese of the Camembert type, but in 1930 (The Penicillia, 310–312) he accepted Bainier's species and reduced *P. camemberti* var. *rogeri* to synonymy. The culture returned to us undoubtedly represents the form sent to Baarn by Thom.

Penicillium caseicolum appears as the ripening agent in a certain portion of the Camembert cheese industry both in France and in the United States. It was discussed by Epstein (Arch. f. Hyg. **45:** 360, 1902) as *P. album* Preuss. About the same time in France, Georges Roger (Revue Hebdomidaire (Paris) **7:** 334. 1903) used *P. caseicolum* Bainier but called it *P. candidum* Link in his patented process. The same usage appears in Mazé's paper (Ann. Inst. Past. **19:** 378–403, 481–491. 1905). Wehmer (in Lafar's Hdb. Tech. Myk. 2 aufl. **4:** 226) called it *P. rogeri*. Later (1910) Thom, with the same organism from imported Camembert cheese, called it *P. camemberti* var. *rogeri*. There seems to be little doubt that Bainier's designation, accompanied by a satisfactory description of the species, is the correct usage.

Penicillium camemberti Thom, in U. S. Dept. Agr., Bur. Anim. Ind., Bul. 82, p. 33, fig. 1. 1906; *Ibid.*, Bul. 110, p. 50, fig. 16. 1910; The Penicillia, pp. 312–313, fig. 44B. 1930.

Synonyms: *P. camembert* Sopp, in Monograph pp. 179–180, Taf. XIX, fig. 134 and Taf. XXIII, fig. 17–18. 1912.

P. aromaticum III Sopp, in Centbl. f. Bakt. etc. II, **4:** 161–169. 1898; cited in Sopp's Monograph, p. 179, 1912, without description but as synonym of *P. camembert* Sopp.

Colonies on Czapek's solution agar (Col. Pl. VII) growing more or less restrictedly, about 2–3 cm. in 10 days to two weeks at room temperature, loose-textured, floccose, cottony (fig. 110C), pure white at first, changing to pale gray-green near glaucous to greenish glaucous (Ridgway, Pl. XLI) after 7 to 8 days, deeply lanose throughout, hyphae not tending to form ropes or fascicles; reverse uncolored or in cream to very pale yellow shades; odor pronounced, simulating that of potato peels; exudate not produced, or present as scattered, small, uncolored droplets largely submerged in the mycelial mass; penicilli fairly abundant, asymmetric, with conidial chains forming an irregular, tangled mass, commonly measuring from 50 to 80μ in length, but with individual structures ranging from 30 to 100μ in length, borne upon long conidiophores arising from the substratum or upon short branches from aerial hyphae; conidiophores more or less tangled, extremely variable in length, ranging from 250 to 600μ by 2.5 to 3.5μ when arising from the substratum, 40 to 200μ in length when borne on aerial hyphae, with walls of conidiophores and fruiting branches commonly slightly roughened; spore-bearing apparatus ranging from 25.0 to 50.0μ in length, irregularly branched, with branches and metulae often poorly differentiated; branches commonly 12.0 to 18.0μ by 2.2 to 3.4μ; metulae borne at different levels in the penicillus and usually in groups of 2 or 3, ranging in size from 9 to 14μ by 2.2 to 3.2μ; sterigmata in groups of 2 to 5, rarely more, 9.0 to 14.0μ by 2.2 to 2.8μ; conidia elliptical when first formed, becoming subglobose at maturity, commonly measuring 3.5 to 5.0μ by 3.0 to 4.5μ, smooth-walled, lightly colored in mass.

Colonies on steep agar essentially as on Czapek but growing somewhat more rapidly and somewhat heavier sporing; conidiophores commonly measuring 1 mm. in length and penicilli slightly larger than described above.

Colonies on malt extract agar growing more rapidly, up to 5.0 cm. in 10 days to 2 weeks (fig. 110D), looser textured and appearing coarser in gross colony aspect; conidiophores up to 2 mm. in length; penicilli averaging somewhat larger than on Czapek, commonly 50 to 60μ or more in

PLATE VII

TOP: Penicillium camemberti Thom, NRRL 877, on Czapek's solution agar, 14 days. *CENTER: Penicillium lanoso-coeruleum* Thom, NRRL 888, on Czapek's solution agar, 12 days. *BOTTOM: Penicillium lavendulum* Raper and Fennell, NRRL 2146, on Czapek's solution agar, 10 days. (Color photographs by Haines, Northern Regional Research Laboratory. Reproduced through co-operation of Chas. Pfizer & Co., Inc.)

length; conidiophores and fruiting branches more conspicuously roughened, but colony coloration essentially as above.

Species description based upon NRRL 877, Thom's No. 5, isolated by him in Storrs, Connecticut, in 1904 from French Camembert cheese. The strain has remained in continuous laboratory culture since that time without apparent change in cultural appearance or structural details. Strain NRRL 878, from the Biourge Collection as *Penicillium camemberti* (Biourge's No. 5), is equally representative of the species. A culture of *P. camemberti* received from the Centraalbureau as having come from Thom in 1931 duplicates NRRL 877 in all particulars, and in all probability originated from Thom's No. 5 since that culture was widely distributed.

Strain NRRL 1740 received in 1941 from Professor Hastings of the University of Wisconsin as *Penicillium caseicolum* is believed to represent a variant of *P. camemberti*. It differs from the species in producing looser textured colonies with conidiophores generally somewhat coarser and colony colors near tilleul-buff (Ridgway, Pl. XL) and showing no bluish green. The reader should bear in mind that *P. camemberti* and *P. caseicolum* are closely related and in cheese manufacture are used to produce essentially the same type of products which carry the same name. It is not, therefore, surprising that variant strains more or less intermediate between the two are occasionally encountered.

The Camembert cheese mold with its pale green conidia appears first in the literature variously as *Penicillium aromaticum* III or *P. aromaticum casei* III in Johan-Olsen's (Sopp) discussion of cheese ripening (1898). No adequate description appeared. Later the French workers, notably Mazé (1905), called it *P. album*. He used *P. candidum* Link for the pure white form, but without diagnosis, and ignored the previous use of the name *P. album* by Preuss (1851). Thom found the form with gray-green conidia to be the dominant organism present upon the surface of the better grades of imported Camembert and demonstrated its function in cheese ripening—hence his description and application of the name to the responsible fungus in 1906. Sopp included it in his Monograph (1912) as *P. camembert*. In the cheese industry in Normandy, *P. camemberti* is used more commonly than *P. cascicolum*, and produces a softer cheese preferred by many judges (fig. 111).

Drewes (1937) reported a *Penicillium* somewhat different from *P. camemberti* to dominate the microflora of "sauermilchkäse." The name *P. henebergi* was proposed but no adequate description was offered.

Occurrence and Significance

The Camembert-Brie group of cheeses, originating in northern France, obtain their texture and flavor from the proteolytic activity of molds be-

longing to this series. Furthermore, the physiological adaptation of these two species to the production of cheese is so close that they are thus far unknown outside the dairy manufacturing industry. In the cheese factory, they dominate, overgrow, and suppress competing forms if the cheese contains a favorable water content, if the humidity is maintained around 88 percent, and if the temperature is maintained at a proper level. Any wide departure from either condition is commonly followed by the de-

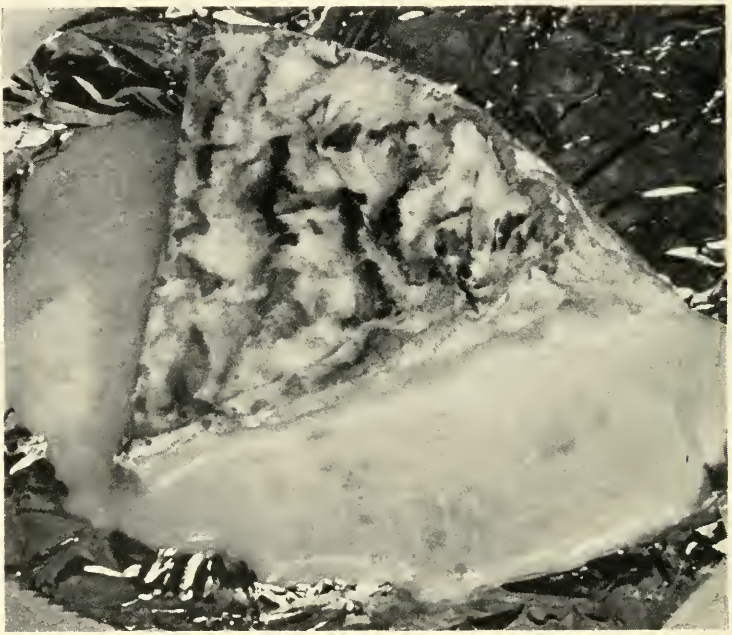


FIG. 111. Camembert cheese. Note the semi-fluid consistency of the cheese which is characteristic of a well ripened and high quality product. (After Thom, in Jour. N. Y. Bot. Garden 1944.)

velopment of other microorganisms, particularly *Scopulariopsis brevicaulis* (Sacc.) Bainier, to the detriment of the resulting cheese.

In the manufacture of these cheeses, the freshly made curd is fashioned or molded into thin cakes, salted upon the surface, and inoculated with the mold, or placed in a room in which the spores of the mold reach the surface from their abundance in the atmosphere. The cheese contains 55 to 60 percent moisture at the outset and is exposed upon mats or boards in a humid ripening room at temperatures preferably from 50° to 60°F. (optimum at 13° to 14°C.). The entire surface becomes covered in about a week with a floccose white covering of mold, perhaps 1 or 2 mm. deep. In about ten days the mold shows a characteristic bluish or greenish gray cast from the developing conidia, if *Penicillium camemberti* is used, or

remains white if the mold is *P. caseicolum*. At about the same time, the curd in contact with the mycelium begins to soften to a smooth buttery texture which gradually extends from all sides toward the center of the mass (fig. 111). The curd is at first markedly acid to litmus but becomes alkaline to litmus as the softening progresses inward. In a period varying with the water content of the mass, the temperature and the humidity, (in commerce usually about four weeks), the entire mass is softened by *P. camemberti*. In Dox's studies (1908, 1909, 1910a) the change was found associated with the elaboration of a proteolytic enzyme similar to erepsin.

Penicillium caseicolum Bainier produces the same type of cheese as *P. camemberti* but of somewhat firmer texture and to most connoisseurs a less attractive flavor.

So long as the industry was restricted to the comparatively localized region in Northern France where it developed, the problems of propagation and control were not significant. Attempts to develop Camembert manufacture in other regions of France and in Germany, however, necessitated investigations to overcome the handicaps of infection by other organisms in factories subject to different climatic conditions. These difficulties were even greater when the task of establishing an industry was attempted in America (Thom 1909, 1945). Successful manufacture in this country was accomplished only when environmental conditions similar to those actually prevailing in northern France were artificially produced (Thom and Fisk, 1918).

Cheeses of the Camembert type have never gained wide popularity in the United States, hence the amount of study devoted to these products and to the molds used in their manufacture has been rather limited. Chief biochemical interest in *Penicillium camemberti* and *P. caseicolum* rests in the enzymes that they produce. Dox (1908, 1909, 1910a) paid particular attention to proteolytic enzymes and their relation to cheese ripening. Ayres and Niedercorn (1942) obtained a patent covering the commercial production of proteolytic enzymes by *P. camemberti*. Robbins (1916) reported on certain factors influencing diastase production in the same species. Dox (1910b) investigated catalase production in numerous species of *Aspergillus* and *Penicillium*, including *P. camemberti*.

Sartory, Sartory and Meyer (1927) studying the optimum pH of different molds reported *Penicillium caseicolum* to grow best at 6.5 to 7.0.

Penicillium commune Series

Outstanding Characters

Colonies on Czapek's agar growing fairly rapidly, typically loose-textured, floccose, comparatively deep, commonly up to 1 or 2 mm., usually medium to heavy sporing with conidial areas in dull bluish green or yellowish green shades, with vegetative hyphae and conidiophores

comparatively coarse and characteristically separate, occasionally showing limited aggregation into ropes or fascicles; colony reverse usually colorless or developing dull yellowish or drab shades.

Conidiophores arising from the substratum or from the mycelial felt, comparatively coarse in most species, often long, up to 500μ or more, and in some species and strains 1 mm., usually unbranched except in the terminal area, with walls typically roughened.

Penicilli comparatively large, asymmetric, often irregularly branched with metulae and sterigmata commonly borne at different levels in the penicillus.

Conidia usually smooth-walled, comparatively large, variable in form from subglobose to elliptical, usually borne in tangled chains and forming irregular masses.

Odor pronounced, moldy, in some strains unusually strong.

Series Key

B. Colonies quickly developing some shade of green in conidial areas.
P. commune series

1. Floccose mycelium uncolored and with reverse uncolored or in drab shades, usually heavily sporing on malt agar.
   a. Conidia globose or nearly so, less than 4.0μ in diameter, finely roughened.
   P. lanosum Westling
   b. Conidia elliptical or in age becoming subglobose, commonly up to 4.0μ or more in diameter, smooth-walled.
      1′. Conidial areas in rather bright yellow-green shades.
      P. lanoso-viride Thom
      2′. Conidial areas bluish green to gray-green.
         aa. Conidial areas with blue element pronounced, near bluish glaucous, deeply floccose..... *P. lanoso-coeruleum* Thom
      3′. Conidial areas with green to gray-green shades predominating; at first court gray to gnaphalium green, becoming olive in age.
         aa. Colonies with unusually strong actinomyces-like odor.
         P. biforme Thom
         bb. Colonies with odor less pronounced.
            1″. Colonies forming a felt 300 to 1000μ deep..... *P. commune* Thom
            2″. Colonies deeply floccose, 1 to 2 mm. deep.
            P. lanoso-griseum Thom

2. Vegetative mycelium yellow to orange, at least adjacent to the substratum; reverse orange to bay; non-sporulating or very lightly sporulating on malt agar.
   a. Colonies deep, 2.0 to 3.0 mm., loosely floccose, lightly sporulating upon Czapek and steep agars..... *P. aurantio-candidum* Dierckx
   b. Colonies thinner, definitely fasciculate, usually heavily sporing on Czapek and steep agars..... *P. aurantio-virens* Biourge
   (in *P. cyclopium* series, p. 503)

Members of the series appear to be limited in nature since they occur rather infrequently among cultures isolated from soil or among the acces-

sions contributed by workers outside this Laboratory. Two of the species recognized are known only from the type strains which have been maintained in laboratory culture for many years. Members of this series, like the Camembert cheese molds, appear to be comparatively stable in culture.

Seven species are recognized, and these may be differentiated in the manner outlined in the general key to the Lanata, a portion of which is reinserted above.

The series is probably artificial in character, and it is entirely possible that certain species are more nearly related to forms included in other sections than to other members of the present series. *Penicillium lanosoviride* Thom, for example, bears a striking resemblance to *P. psittacinum* Thom in the Funiculosa and likewise to certain members of the *P. viridicatum* series in the Fasciculata. The possibility that all of these species represent members of a single natural group should not be overlooked.

There are striking resemblances between Thom's species *P. commune* and *P. biforme*, that are included here, and *P. puberulum* Bainier which Thom in 1930 placed in the Velutina and which we now assign to the *P. cyclopium* series in the Fasciculata. Similarly, *P. aurantio-candidum* Dierckx, included here because of its deep lanose colonies, shows striking resemblances to *P. aurantio-virens* Biourge, a fasciculate species also included in the *P. cyclopium* series.

Differences in colony texture and pattern may lack the basic significance that we tend to attribute to them in our present system of classification. Fully cognizant of this possibility, we still feel that the bases employed are the most satisfactory developed up to this time. While certain species and strains may be keyed away from closely related species, we believe that the number of such errors is limited. We have considered the desirability of withdrawing the present Section completely and assigning individual species to different series in other sections, primarily in the Fasciculata, to which they seem to be most nearly related. While such a course might be desirable from the viewpoint of evolution, we regard it as impractical for this Manual, the primary purpose of which is to enable mycologists to identify recognizable species of Penicillia. In any study of the biochemical potentialities of members of this series, the investigator is advised to examine carefully those species in other sections which are cited as possibly closely related in the brief discussions that follow the descriptions of individual species.

Penicillium lanosum Westling, in Arkiv för Botanik **11:** 55, 97–99, figs. 18 and 60. 1911. Thom, The Penicillia, pp. 317–318. 1930.

Colonies on Czapek's solution agar attaining a diameter of 2.5 to 3.0 cm. in 10 to 12 days at room temperature, consisting of a floccose over-

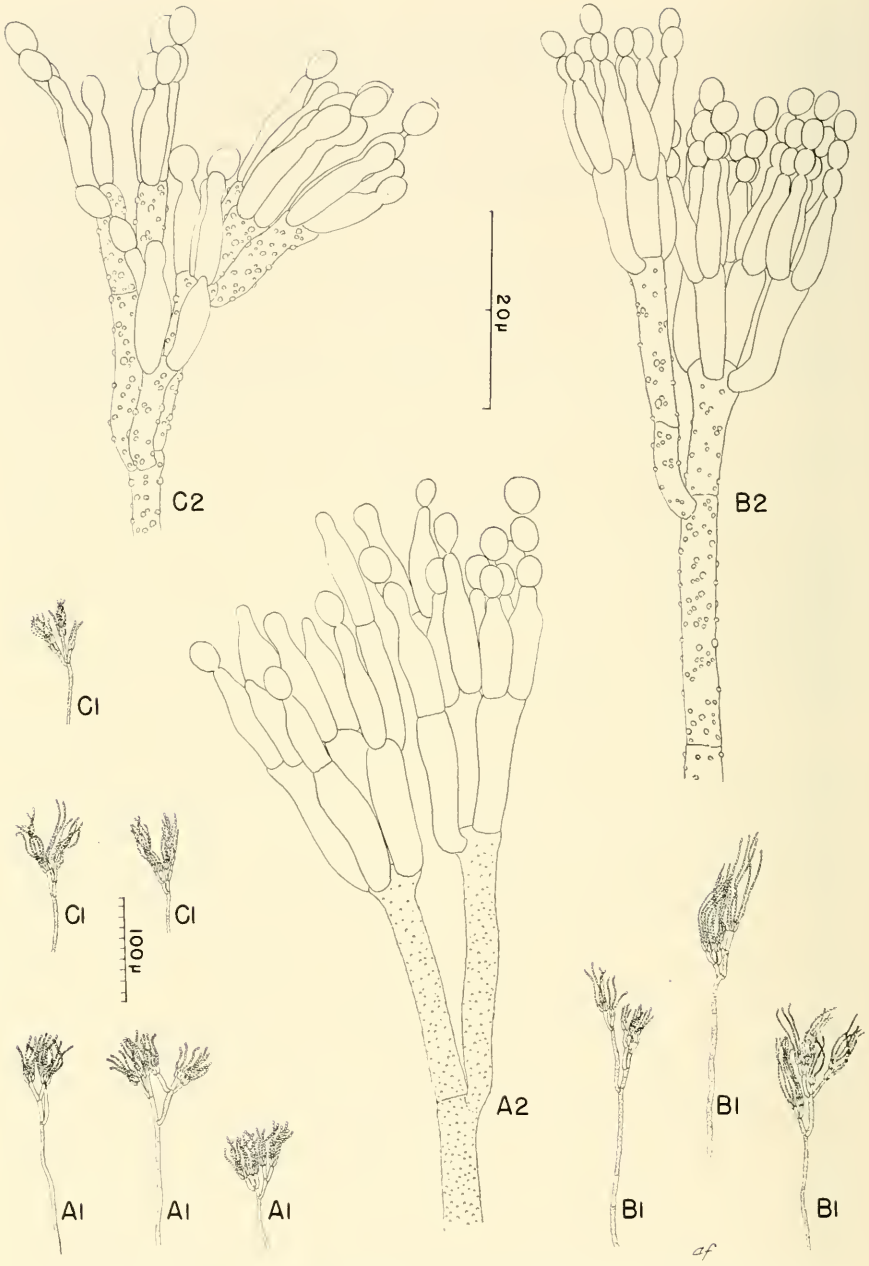


FIG. 112. *Penicillium commune* series. A_1, Habit sketches and A_2, detailed drawings of typical penicilli in *P. lanoso-viride* Thom. B_1, Habit sketches and B_2, detailed drawing of representative penicilli in *P. lanoso-coeruleum* Thom. C_1 and C_2, The same of *P. commune* Thom.

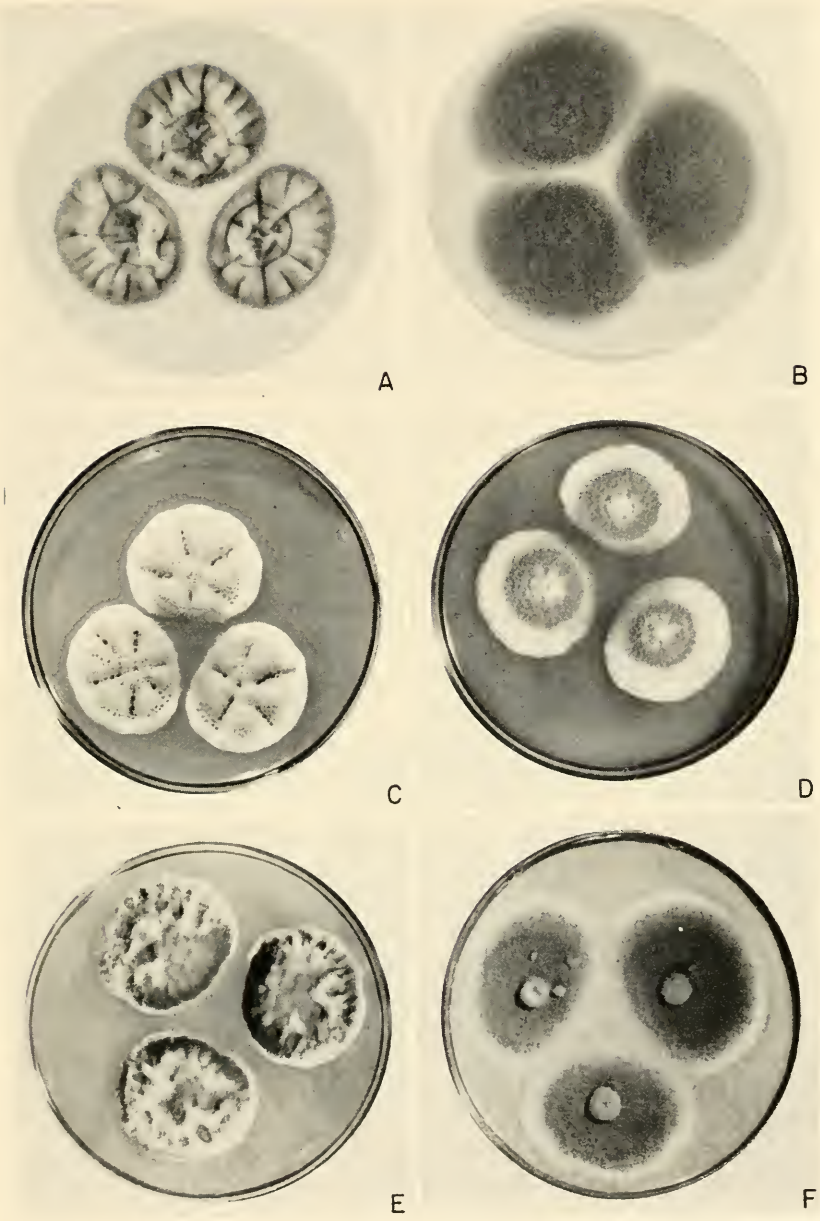


FIG. 113. *Penicillium commune* series. *A* and *B*, *P. lanosum* Westling, NRRL 2009, on Czapek and malt agars at two weeks. *C* and *D*, *P. lanoso-viride* Thom, NRRL 879, as the preceding. *E* and *F*, *P. lanoso-coeruleum* Thom, NRRL 888, as above.

growth arising from a tough mycelial felt, irregularly wrinkled (fig. 113A), with central or subcentral colony areas commonly raised, 1 to 2 mm. deep, producing conidial heads most abundantly in marginal zones with central areas white to very light gray, fruiting areas in pale green to glaucous gray shades near dark glaucous gray (Ridgway, Pl. XLIII) or court gray (R., Pl. XLVII); exudate lacking or limited; odor lacking or indefinite; reverse colorless to light yellowish drab shades; conidiophores arising mostly as short branches from aerial hyphae 100 to 200μ in length, less commonly from the substratum and ranging from 250 to 600μ by 2.5 to 3.0μ with walls smooth or delicately roughened; penicilli comparatively large, asymmetric, irregularly branched and tending to become divergent, bearing tangled and irregular spore masses up to 50 to 75μ in length; branches variable, commonly 10 to 20μ by 2.0 to 2.5μ, occasionally longer, often arising low on the conidiophore and not appearing as an integral part of the terminal penicillus; metulae few in the verticil, about 8 to 12μ by 2.0 to 2.5μ, commonly borne at different levels; sterigmata borne in clusters of 5 to 10, measuring about 7.0 to 8.5μ by 2.0 to 2.5μ, definitely constricted at the point of spore origin; conidia globose to subglobose, 2.5 to 3.0μ in diameter with walls finely granular, appearing dull gray-green in mass.

Colonies on steep agar growing more rapidly, attaining a diameter of 3.5 cm. in 10 days, marginal zones 1 to 2 mm. wide, white, shading through court gray and gnaphalium green (R., Pl. XLVII) to storm gray (R., Pl. LII), with the development of mature penicilli, otherwise as on Czapek except sporulating more abundantly and producing somewhat more exudate as small colorless drops embedded in the colony; penicilli as on Czapek but commonly larger.

Colonies on malt agar about 2.5 to 3.0 cm. in diameter, plane, loose-textured, heavily sporulating (fig. 113B), with conidiophores arising from the substratum and presenting the aspect of a deep velvety colony, colony coloration as on steep agar; penicilli as described above.

Species description based primarily upon NRRL 2009, a culture received from the Centraalbureau as Westling's strain of this species; presumably type. Numerous cultures have been examined by us which are characterized by lanose colonies that run through a series of gray-green shades in the growing period and which produce conidia generally 3.0μ or less in diameter. The tendency of these forms to produce penicilli more or less divaricate and the faint roughening of the conidia suggests relationship to the Divaricata.

Penicillium lanoso-viride Thom, in The Penicillia, pp. 314–315. 1930.

Colonies upon Czapek's solution agar attaining a diameter of 2.5 to 3.0 cm. in 10 to 12 days at room temperature, azonate or with traces of

zonation in marginal areas only, floccose, about 1–2 mm. deep, conspicuously marked by deep radial furrows (fig. 113C), with marginal areas broad and white during the growing period, conidial areas at first in rather bright green shades such as water green, grape green or pois green (Ridgway, Pl. XLI), fading unevenly to light shades of olive gray in age; exudate abundant, in small colorless drops, partially embedded in the mycelial mass; odor pronounced, penetrating; reverse uncolored or tardily and unevenly developing drab shades; conidiophores arising from the substratum or from aerial hyphae, up to 1000μ by 4.0 to 5.0μ, more or less sinuous or flexuous, with walls conspicuously roughened; penicilli about 40 to 50μ long with walls of lower elements commonly roughened, asymmetric, irregularly branched and bearing tangled chains of conidia (fig. 112A_1); with metulae produced at different levels and variously duplicated by secondary metulae, often producing sterigmata at several levels; both metulae and sterigmata tending to fall away in mounted preparations from older areas; branches 20 to 40μ long, more or less divergent; metulae 15 to 20μ long with apices usually enlarged (fig. 112A_2); sterigmata mostly 10 to 12μ, less commonly 14 to 18μ by 3.0 to 4.0μ in diameter, often tapering gradually to rather long tubes; conidia globose to subglobose, mostly about 4.0 to 4.5μ in diameter but occasionally showing cells much larger and more or less elliptical, smooth, thin-walled.

Colonies upon steep agar growing more luxuriantly, attaining a diameter of 3.0 to 4.0 cm. in 10 to 12 days, but showing the same general growth characteristics and coloration as on standard Czapek's agar; penicilli commonly larger than above, measuring up to 75 to 80μ in length but similar in pattern.

Colonies upon malt extract agar appearing somewhat thinner and less floccose than upon the above substrata, but with conidial areas similarly colored (fig. 113D); in marginal areas often showing a suggestion of fasciculation with the conidiophores and some ascending sterile hyphae tending to aggregate into poorly defined clusters or bundles; fruiting structures often less completely branched, but with individual parts generally larger.

The type culture, NRRL 879 (Thom No. 5034.12), was received in January 1939 from J. H. Birkinshaw, Nobel Explosives Company, as an isolate from the "sweet waters" of a glycerine still at Ardeer, Scotland. Colonies of the type show a striking resemblance to *Penicillium psittacinum* Thom in the bright "parrot-green" colors developed in conidial areas on certain substrata, particularly malt agar. It differs from that species, however, in lacking distinct zonation, and in lacking the ropes of hyphae clearly evident at the edges and over the surface of the older colonies of *P. psittacinum*. Its coloration and the general characteristics of its fruiting structures is also suggestive of the *P. viridicatum* series, a possible relationship that is further indicated by the tendency to become fascicu-

late in older cultures on malt extract agar. NRRL 930, received from Professor Macy as an unidentified *Penicillium* is believed to represent a floccose, lightly sporulating variant of *P. lanoso-viride* Thom. A strain obtained under this name from the Centraalbureau, in May 1946, received by them from Thom in 1936 and probably stemming from the type culture, duplicates the above in all essential details but retains the bright green colors over a longer period.

Penicillium lanoso-coeruleum Thom, in The Penicillia, pp. 322–323. 1930.

Colonies upon Czapek's solution agar (Col. Pl. VII) growing fairly rapidly, about 4.0 to 5.0 cm. in diameter in 10 to 12 days at room temperature, deeply floccose, up to 5 mm. in deepest areas (fig. 113E), with surface very uneven, appearing deeply ridged or broadly tufted, azonate or nearly so, with growing margin white, 2.0 to 3.0 mm. wide, with conidial areas shading from bluish glaucous at the margin to deep bluish gray-green in the denser areas (Ridgway, Pl. XLII), with blue coloration pronounced; exudate limited, clear; odor not pronounced but moldy; reverse uncolored or in dull yellowish buff shades; conidiophores arising primarily from the aerial felt, mostly 200 to 600μ by about 3.0μ, sometimes longer, with walls pitted or delicately roughened; penicilli asymmetric, commonly consisting of a terminal verticil of metulae or showing one or more branches with verticils of metulae and sterigmata (fig. 112B_2) and bearing conidial chains in a loosely columnar or tangled mass (fig. 112B_1), sometimes up to 200μ or more in length; branches extremely variable, from 7.0 to 25.0μ in length but mostly 10.0 to 15.0μ by 2.8 to 3.3μ; metulae in verticils of 3 to 5, mostly 10 to 15μ by 2.5 to 3.0μ; sterigmata few in the verticil, about 8.0 to 10.0μ by 2.0 to 2.5μ; conidia showing some ellipticity, up to 3.5 or even 4.0μ by 2.5 to 3.0μ, less commonly subglobose, smooth-walled.

Colonies on steep agar growing somewhat more rapidly than on Czapek but essentially duplicating the above in texture and general appearance, sporulating more heavily and more quickly developing gray shades; exudate limited, clear; odor pronounced, somewhat moldy; reverse uncolored or in light yellowish orange shades; penicilli as described above.

Colonies on malt extract agar, heavily sporing throughout, plane, deeply lanose with conidiophores arising largely from the substratum (fig. 113F), with conidial areas in fairly bright yellow-green shades near sage green (R., Pl. XLVII) or Russian green (R., Pl. XLII); exudate lacking; odor pronounced moldy; reverse in golden yellow shades; penicilli as described above.

Species description centered upon the type, NRRL 888, from the Thom Collection as No. 2543a. This culture was isolated originally as a deeply

floccose contaminant in a culture of *Penicillium cyclopium* from Westling. The name was selected to indicate a floccose or lanose species in shades of blue-green with the blue strongly evident although not very satisfactorily represented by Saccardo's "coeruleus". The species is known only from the type strain. A culture received from the Centraalbureau under this name as Thom's type differs only in producing tardily sporing colonies.

Penicillium biforme Thom, in U. S. Dept. Agr., Bur. of Anim. Ind., Bul. 118, pp. 54–55, 1910; Thom, The Penicillia, pp. 320–322, fig. 45. 1930.

Colonies on Czapek's solution agar approximately 3.5 to 4.0 cm. in 10 to 12 days at room temperature, deeply floccose especially in central areas with marginal portions radiately furrowed (fig. 114A), at first white but becoming slowly gray to greenish gray with the development of abundant fruiting structures, at times with a faint flesh or rosy tint in marginal or submarginal areas of predominantly vegetative growth; exudate colorless or lacking; reverse colorless; odor very strong and suggesting the presence of an actinomycete; conidiophores mostly 75 to 200μ by 3.0 to 3.5μ, occasionally longer, arising from the substratum or from aerial hyphae, with walls roughened; penicilli comparatively small and consisting a limited number of elements, commonly about 40 to 50μ in length, irregularly branched, asymmetric, with branches divergent or appressed and measuring about 15 to 20μ by 3.0 to 3.5μ, with metulae and sterigmata borne at various levels, bearing conidia in tangled chains; metulae limited in number, usually in groups of 2 to 5, about 10 to 12 by 3.0 to 3.5μ; sterigmata in small clusters, commonly 3 to 5 in number and measuring about 8 to 10μ by 2.5 to 3.0μ, abruptly narrowed in the apical area; conidia cylindrical to elliptical when first formed, remaining elliptical or becoming subglobose, rarely globose when mature, mostly 3.5 to 4.0μ in long axis, occasionally larger, smooth-walled, light grayish green in color.

Colonies on steep agar about 4 cm. in diameter in 10 to 12 days, deeply floccose, at first white, becoming dull gray-green near storm gray (Ridgway, Pl. LII) with the development of conidial structures; conidiophores longer than above, commonly ranging up to 300μ by 3.0 to 4.0μ, bearing penicilli usually larger than on Czapek but of the same general character; conidia appear subglobose to slightly elliptical, smooth-walled, commonly 3.5 to 4.0μ.

Colonies on malt extract agar, 4.5 to 5.0 cm. in 10 to 12 days, heavy-sporing (fig. 114B), deeply floccose in central area, less conspicuously so in marginal areas, more or less zonate, commonly appearing somewhat tufted or funiculose; conidiophores arising mostly from the substratum in

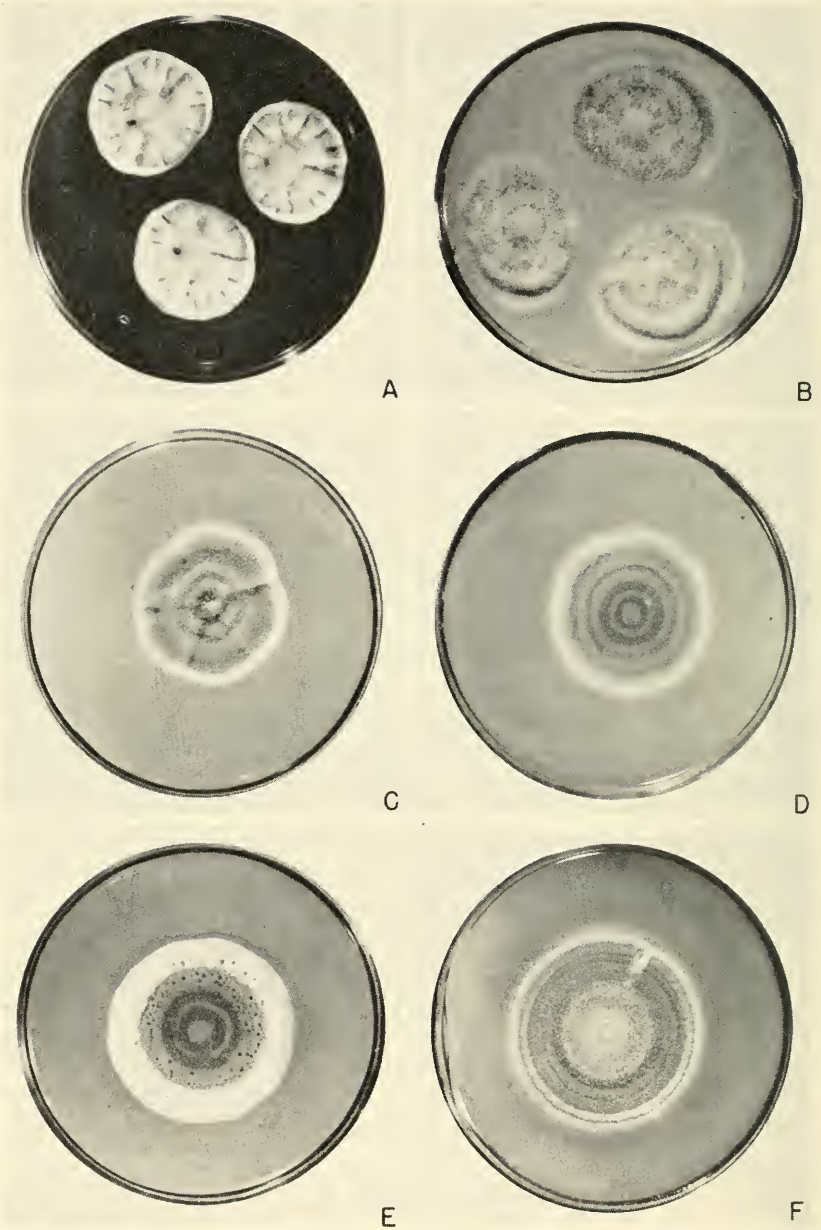


FIG. 114. *Penicillium commune* series (continued). *A* and *B*, *P. biforme* Thom, NRRL 885, on Czapek and malt agar at two weeks. *C* and *D*, *P. commune* Thom, NRRL 890, as the preceding. *E* and *F*, *P. lanoso-griseum* Thom, NRRL 894, as above.

a fairly close stand, with dimensions as on steep agar, conspicuously roughened; penicilli generally larger than above and regularly more elaborately branched.

This species is characterized particularly by its dull, gray-green conidial areas and its strong, penetrating actinomyces-like odor which is especially pronounced on Czapek's solution agar.

Represented in our Collection by the type strain, NRRL 885 (Thom's No. 39). This culture was isolated by Thom in 1904 from cheese and has retained its distinguishing cultural characteristics since that time. A culture received from the Centraalbureau in 1946 as Thom's culture of *Penicillium biforme* represents a deeply floccose, essentially white, sparsely sporulating strain which may or may not represent a cultural variation from the original; penicilli, when produced, duplicate essentially those of NRRL 885 but the odor is much less marked than in the typical culture. The species bears a striking resemblance to *P. commune* Thom, and in cultural appearance is likewise suggestive of *P. puberulum* Bainier (see p. 497).

Penicillium commune Thom, in U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, pp. 56–57, fig. 19. 1910; Thom, The Penicillia, pp. 324–325, figs. 46 and 47. 1930.

Colonies on Czapek's solution agar attaining a diameter of 3.0 to 4.0 cm. in 10 to 12 days at room temperature, floccose, with mass of mycelium about 500 to 700μ deep, marginal zone white, about 2 mm. wide (fig. 114C), followed by zones of gray-green, court gray, gnaphalium green and pea green (Ridgway, Pl. XLVII) becoming olive-gray to mouse gray in age (R., Pl. LI), at times showing few to several shallow radiate furrows, spreading evenly as submerged and aerial hyphae at colony margins and quickly developing into a complex felt of branching hyphae, the resulting felt being rather tough and showing at the margin a trace of fasciculation or ropiness (suggestive of *Penicillium solitum*); exudate colorless, limited, and enmeshed in the floccose mycelial mass; odor fairly strong, "moldy"; reverse colorless or yellowish, sometimes with traces of rose; conidiophores varying from very short up to 500μ by 5.0μ in marginal areas of older colonies, with walls finely roughened to coarsely granular in age, bearing penicilli 40 to 50μ in length and ranging up to 80μ; penicilli branched, asymmetrical (fig. 112C_2), characterized by appressed branches and metulae often borne at different levels, conidial chains tending to form compact masses at first but often diverging in age to produce a loose tangled mass (fig. 112C_1); branches variable in dimensions up to 15.0 to 20.0μ in length; metulae 15.0 to 20.0μ by 3.0 to 3.5μ; sterigmata few in the verticil, usually produced at approximately the same level, measuring

10.0 to 12.0μ by 3.0μ; conidia elliptical to subglobose, mostly 4.0 to 5.0μ in long axis, smooth-walled.

Colonies on steep agar essentially duplicating those on Czapek in rate of growth and in general colony texture, but showing more numerous and conspicuously radial furrows; exudate production and odor as described above; colony reverse uncolored to light buff; penicilli as on Czapek.

Colonies on malt extract agar duplicating the above in rate of growth, but differing in texture, comparatively thin, plane, zonate, almost velvety, with margins thin, largely submerged (fig. 114D); exudate lacking; odor spicy; reverse uncolored or becoming yellowish in age; penicilli as above.

Species description based upon the type strain, NRRL 890 (Thom's No. 23), which was isolated by Thom from cheese in 1904 at Storrs, Connecticut. The culture has been under continuous laboratory cultivation since that time without significant change in cultural or morphological characteristics. NRRL 891, which represents the same strain sent to Biourge and returned to us, produces thinner, more restricted, and lighter sporing colonies but still retains the basic species characters. Three cultures were received from the Centraalbureau as *Penicillium commune* Thom in February 1946. One of these, labeled "Thom I", and in correspondence indicated to be Thom's No. 23, no longer presents the typical cultural picture of the species. Colonies are relatively close-textured and produce comparatively few and small conidial structures; but spore dimensions remain satisfactory. It is probable that the strain returned to us represents a cultural variant which has developed during the period of laboratory cultivation in Baarn. A second culture, labeled "Thom II" represents Thom's strain 4733.40 as received from Biourge. Culturally it is similar to NRRL 890 but produces more restricted, more strongly furrowed and more heavily sporing colonies. A third culture, labeled "from *Cichorium intybus*, 1944" essentially duplicates the preceding but shows conidial areas in somewhat brighter blue-green shades.

When first described, Thom believed this species to be unusually common in nature, hence the name. Continued study of the genus *Penicillium* has failed to substantiate this belief, and *P. commune* today must be regarded as a rather unique species which is only occasionally encountered. Once recognized, the experienced mycologist should encounter little difficulty in subsequently identifying the species.

Culturally and microscopically *Penicillium commune* bears a striking resemblance to *P. puberlum* Bainier as that species is known from Alsberg and Black's strain, now maintained as NRRL 845. Colonies of NRRL 890 are generally somewhat deeper and of looser-texture, but in general habit and coloration often duplicate almost exactly those of NRRL 845.

Penicillium lanoso-griseum Thom, in The Penicillia, p. 327. 1930.

Colonies upon Czapek's solution agar forming deeply floccose felts 3.0 to 3.5 cm. in diameter and 1 to 2 mm. deep in 10 to 12 days at room temperature (fig. 114E), with growing margins white, several mm. broad, fruiting abundantly with conidial areas in dull green shades ranging from bluish glaucous (Ridgway, Pl. XLII) at the very edge through shades of glaucous blue to shades of olive gray and finally mouse gray (R., Pl. LI), zonation in the form of raised areas commonly becoming more or less evident in older colonies; exudate abundant, as colorless drops enmeshed in the floccose mycelial mass; reverse colorless or faintly yellowish; odor slight; conidiophores variously produced as branches from aerial or from submerged hyphae, up to 1 mm. or more in length by 3.0 to 4.0μ in diameter, with walls pitted to coarsely granular in age; penicilli usually rather compact, often branched with branches variable in length, bearing verticils of metulae and sterigmata and producing conidial chains in more or less columnar masses or variously splitting or becoming tangled in age; metulae 12.0 to 20.0μ long; sterigmata up to 12.0μ by 2.5 to 3.0μ; conidia mostly elliptical, about 4.0 by 3.0μ, smooth-walled, commonly found in chains in mounts.

Colonies on steep agar 3.0 to 3.5 cm. in diameter with surface appearing more or less granular or tufted in 10 to 12 days, deeper than on Czapek, up to 3.0 mm., with broad white margin raised and even more conspicuous, radially furrowed in marginal zones, heavily sporing in central colony area in colors as described on Czapek but maturing more rapidly; exudate less abundant; odor unpleasant; reverse uncolored or in light buff shades; penicilli as described above.

Colonies on malt extract agar duplicating the above in rate of growth, plane, commonly zonate (fig. 114F), with traces of ropiness or fasciculation throughout the entire colony but most conspicuous at the margins, heavily sporing in gray-green shades near gnaphalium green (R., Pl. XLVII); exudate lacking; odor spicy; reverse uncolored or in light buff shades; penicilli as described above.

Species description based upon the type, NRRL 894 (Thom's No. 2746.2a from leaf mold collected for him by C. J. Koning in "Spanderswoud" near Bussum, Holland, in 1913). NRRL 886, isolated from dairy products by Professor Macy, University of Minnesota duplicates the above culture closely enough to warrant consideration with it. NRRL 886 grows more rapidly and produces a larger colony than NRRL 894, but in other details the two strains seem to duplicate one another.

The name is used to designate a deeply lanose species with gray conidial

areas. *Penicillium lanoso-griseum* is obviously closely related to *P. commune* Thom, and differs from the latter primarily in producing much deeper colonies. The significance of this difference is somewhat questioned, since a strain returned to us in May 1946 by the Centraalbureau as a culture from Thom in 1930 (and presumably the type) is culturally and microscopically almost indistinguishable from the type of *P. commune* as maintained at this Laboratory. It is possible that the description of *P. commune* Thom should be broadened to include forms now regarded as representative of both species.

Penicillium aurantio-candidum Dierckx, in Biourge, Monograph, La Cellule **33:** 116–119; Col. Pl. I; Pl. II, fig. 4, Pl. XXIII, fig. 136. 1923. Thom, The Penicillia, pp. 319–320. 1930.

Probable Synonym: *P. aurantio-albidum* Biourge, in Monograph, La Cellule **33:** fasc. 1, pp. 197–198; Col. Pl. III and Pl. V, fig. 28. 1923. Thom, The Penicillia, p. 322. 1930.

Colonies on Czapek's solution agar at 25°C. attaining a diameter of 2.0 to 2.5 cm. in 10 days, deeply floccose up to 2.0 to 3.0 mm. in central areas, thinning only slightly at the margin, showing few shallow, radial furrows, loose-textured, at first white, becoming glaucous blue to greenish glaucous blue (Ridgway, Pl. XLII) with the development of mature penicilli, finally gray in age near storm gray (R., Pl. LII); little or no exudate produced; odor pronounced, "moldy"; reverse in orange or orange-red shades becoming Sanford's brown or auburn to mahogany red or bay in age (R., Pl. II); with agar becoming conspicuously colored in broad zones beyond the colony margin during the growing period; conidiophores variable in length up to 1 mm. or more by 3.5 to 4.0μ or 4.5μ in diameter, appearing smooth or finely roughened, supporting large penicilli up to 50 to 60μ in length bearing tangled chains of conidia 50 to 75μ long; penicilli much branched, asymmetric, irregular in pattern with branches, subbranches, and metulae of varying length commonly occurring in the same penicillus, hence, bearing sterigmata and conidia at different levels; branches commonly 10 to 20μ by 3.0 to 3.5μ; metulae commonly 10 to 12μ by about 3.0 to 3.5μ; sterigmata about 7.0 to 9.0μ by 3.0 to 3.5μ; conidia smooth-walled, elliptical to subglobose with ellipticity generally evident when viewed in chains, mostly 3.0 to 3.5μ by 2.5 to 3.0μ, larger individuals occasionally seen.

Colonies on steep agar growing more rapidly, about 3.5 cm. in 10 days, deeply floccose up to 3 to 4 mm., slightly furrowed, bearing abundant conidiophores and colored as on Czapek; no exudate produced; odor more

pronounced, "moldy"; colony reverse and surrounding agar in red-orange shades, from English red to mahogany red to bay in age (R., Pl. II); penicilli as on Czapek's solution agar.

Colonies on malt agar growing slowly, about 2.5 cm. in 10 days, deeply floccose, white to very light cream, non-sporulating; odor not pronounced; no exudate; reverse in orange-yellow shades near deep chrome through cadmium yellow to raw sienna (R., Pl. III), with agar in surrounding zones in darker shades near mahogany red (R., Pl. II).

The species description is based primarily on NRRL 884 (Thom's No. 4733.6) received from Biourge as *Penicillium aurantio-candidum* Dierckx, and presumably type. The species is represented also by a culture from the Centraalbureau labelled *P. aurantio-albidum* Biourge which had been supplied by Thom in 1931, presumably his No. 4733.4.

In Thom's Monograph (1930), *Penicillium aurantio-candidum* Dierckx as described by Biourge (1923), and *P. aurantio-albidum* Biourge were considered as separate species although cultural similarities were observed at the time. In the recultivation and comparison of these cultures incident to the present study the close relationship of the two forms has become increasingly evident, the two cultures appearing almost identical culturally and microscopically. Both strains are characterized by colonies which become orange to red or brown in reverse, and both are characterized by an intense coloration of the substratum in the same or darker shades which extends into the agar 2 to 3 cm. beyond the colony margin, and thus produces conspicuous zones of reddish brown to mahogany color. This distinctive coloration of the substratum is seen in all common substrata but is most evident upon Czapek's solution agar with or without the addition of steep liquor. It appears to be characteristic of this species, and also of *P. aurantio-virens*, a form probably closely related but assigned to the *P. cyclopium* series because of its definitely fasciculate habit.

Culture NRRL 887 (Thom's 4733.4), the type strain of Biourge's *Penicillium aurantio-albidum*, under continued laboratory cultivation in our hands has become less characteristically lanose and now produces restricted colonies, more or less floccose, often "wet", and characterized by the production of limited conidia on irregular and atypical penicilli. The characteristic pigment is no longer produced and the strain cannot now be regarded as representative of the series.

Occurrence and Significance

Members of the *Penicillium commune* series appear to be comparatively rare in nature. Thom (1910) isolated the type strains of *P. biforme* and *P. commune* from cheese but attributed no special significance to their

presence. Other species were originally isolated from soil or substrates subject to soil or water borne contamination. All appear to be primarily of soil origin.

Pistor (1930) reported *Penicillium commune* as common in forest soils in Germany. Yendo (1926) reported the same species upon silk in various stages of processing, where, with other micro-organisms, it caused a brown discoloration through a series of enzymatic actions on the silk proteins. Brien and Denne (1945) found this species to be common on areas of discolored wall paper in State houses in New Zealand. Effective control was realized by adding 2 percent "santobrite" (Sodium pentachlorophenate) to the glue size or flour paste used as an adhesive. Other investigators have employed *P. commune* as a test organism *per se*. Burnside (1927) found *P. commune* to be prevalent on brood combs and to produce an odor in the hive which destroyed the morale of the bee colony. Pulvertaft and Walker (1939) included it among the organisms investigated for the control of airborne bacteria and fungus spores by aerosols. Lagoni (1941) used it in conjunction with other organisms responsible for the spoilage of butter and margarine in studies on the microbicidal action of diacetyl.

Dox (1910) reported *Penicillium biforme* to produce unusually high yields of catalase when grown in a synthetic medium.

Chapter XI

ASYMMETRICA

Sub-section: FUNICULOSA

Species included in the present section produce colonies ranging from definitely floccose to almost velvety, but typically show part of their aerial hyphae combined into trailing, branching, and usually anastomosing ropes or funicles. Erect fascicles or coremia are not produced. Conidiophores arise in part directly from the submerged mycelium, partly as terminal portions of ascending aerial hyphae, and partly as branches from the characteristic ropes of aerial vegetative hyphae, the latter predominating in certain species and strains. Penicilli are consistently asymmetrical and are usually branched below the level of the metulae, but differ markedly in general pattern between the two series that comprise the section. Certain differences in colony pattern and texture are generally correlated with structural differences in the penicilli.

In one of the series, typified by *Penicillium terrestre* Jensen, the general colony aspect approaches that of the Lanata on the one hand, and of the Fasciculata on the other. Furthermore, in size and pattern, the penicilli of the *P. terrestre* series closely approximate those developed in both of these sections of the Asymmetrica. In the other series, typified by *P. pallidum* Smith, the colonies are generally thinner and commonly develop less aerial growth. The penicilli are commonly narrow, with all cellular elements often laterally appressed and with sterigmata thin, parallel, and closely crowded.

The degree of natural relationship between the *Penicillium terrestre* series and the *P. pallidum* series, is doubtful. Nevertheless, since both produce asymmetrical penicilli, and both are characterized by colonies more or less funiculose, they may be conveniently keyed together. Whereas, the *P. terrestre* series is undoubtedly related to other sections of the Asymmetrica, members of the *P. pallidum* series do not appear to bear close relationship to any recognized series. They seem to represent a group well apart from all others. The possibility that they may represent conidial structures belonging to other genera that have by coincidence assumed a fairly typical penicillate form should not be wholly disregarded, although concrete evidence in support of such a view is lacking.

Key to the Funiculosa

I. Conidial areas in definite yellow-green, blue-green, or gray-green shades; penicilli large, representing the same type as seen in the Lanata and Fas-

ciculata sections; conidiophore walls more or less roughened, but metulae and sterigmata smooth..... *P. terrestre* series 446

A. Colonies with reverse uncolored or in pale yellow to drab shades.

1. Conidia in bright yellow-green shades..... *P. psittacinum* Thom 448
2. Conidia in dull gray-green shades, with conidiophores usually conspicuously roughened..... *P. terrestre* Jensen 450
3. Conidia in blue-green shades, with conidiophores smooth or nearly so. *P. solitum* Westling 453

B. Colonies deeply colored in reverse, in reddish to dark brown shades. *P. resticulosum* Birk., Raist., and Smith 455

II. Conidial areas variously colored, not in green shades; penicilli often comparatively narrow with cellular elements laterally compressed; walls of conidiophores, metulae (and often the sterigmata) are closely and conspicuously roughened..... *P. pallidum* series 458

A. Conidia white to cream colored.

1. Conidial chains divergent, becoming tangled in age. *P. pallidum* Smith 461
2. Conidial chains in well-defined columns..... *P. putterillii* Thom 461

B. Conidia in light to dull gray shades..... *P. namyslowskii* Zaleski 462

C. Conidia in light violet, lavender, or vinaceous shades. *P. lavendulum* Raper and Fennell 464

Penicillium terrestre Series

Outstanding Characters

Colonies spreading, lanose or floccose, with surface growth characterized by abundant and conspicuous ropes or funicles of hyphae when viewed under low magnification, in age sometimes developing true fascicles, and in thin colony areas often appearing velvety.

Conidiophores arising either from ropes of aerial hyphae or from the substratum, often comparatively coarse up to 3.5 to 4.0μ in diameter, with walls usually but not consistently roughened.

Penicilli asymmetric, comparatively large, commonly branched, approximating those of the Fasciculata and the Lanata in size and dimensions.

Metulae, sterigmata, and conidia comparatively large; the latter commonly up to 4.0 to 5.0μ in diameter and often showing wide variation in size in the same mount.

Vegetative mycelium fairly coarse, commonly measuring 4.0 to 5.0μ in diameter.

Series Key

(See General Key to the Funiculosa)

The *Penicillium terrestre* series as considered here consists primarily of forms isolated with considerable frequency from soil. They are characterized by rapidly growing, loose-textured to floccose or lanose colonies, that typically show the production of abundant ropes of aerial vegetative

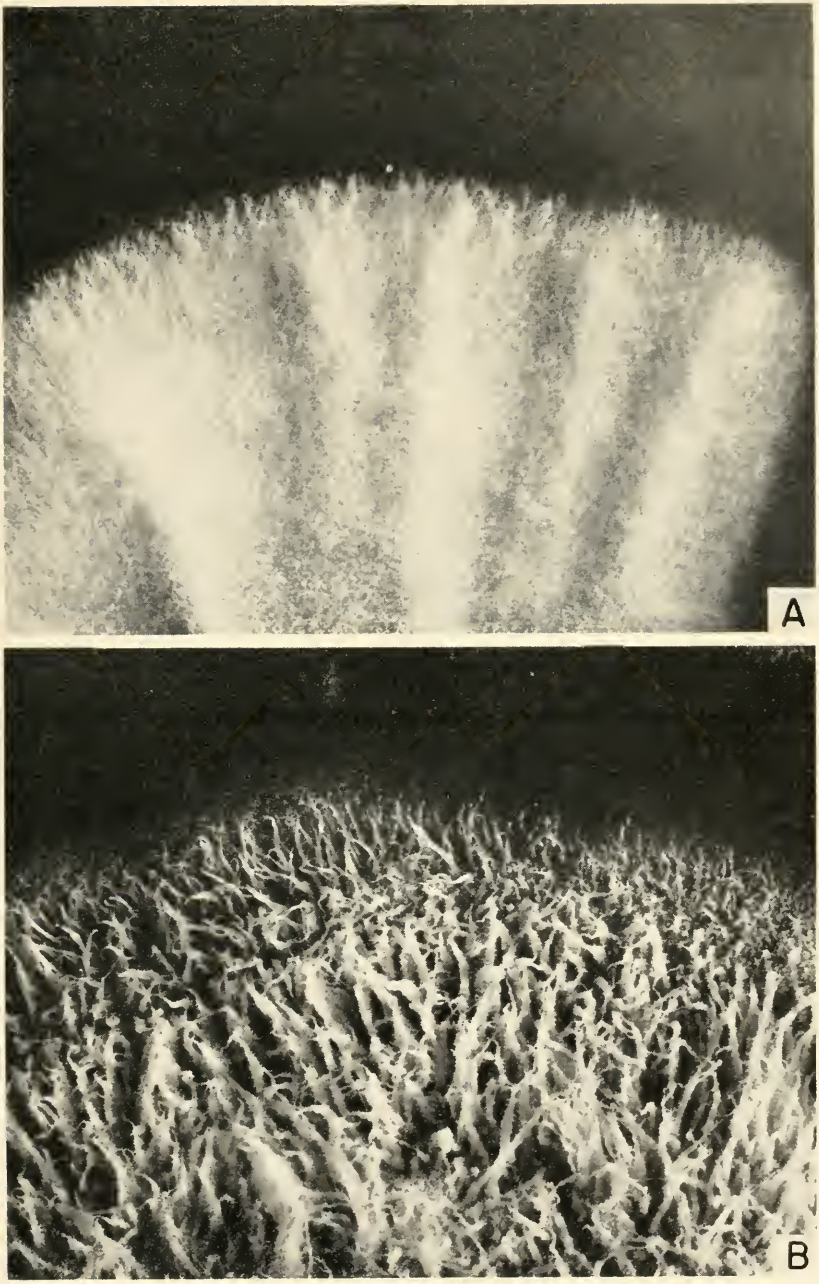


FIG. 115. Funiculose colony margins. *A*, Lightly funiculose margin as seen in *Penicillium resticulosum* Smith, NRRL 2021, on Czapek agar, × 6. *B*, Strongly funiculose margin as seen in *P. pallidum* Smith, NRRL 2156, as seen on steep agar, × 6.

hyphae (fig. 115). They range in color from a fairly bright yellow-green characteristic of *P. psittacinum* Thom, through shades of dull gray-green in many isolates of *P. terrestre* Jensen and in *P. resticulosum* Birk., Raist., and Smith to the dull blue-green shades of *P. solitum* Westling.

Sharp lines of species demarcation do not occur, and there is considerable doubt as to whether all of the forms included should be recognized. A considerable biochemical literature, however, has been built up around the species retained. Furthermore, individual strains can be found which conform quite satisfactorily with the original descriptions and with the treatment given these species by Thom (1930) and other investigators. For these reasons, we believe it is advisable to recognize *Penicillium psittacinum*, *P. terrestre*, *P. resticulosum*, and *P. solitum* and to define them in terms which we believe will permit the user to assign members of this series to one or the other of these species with reasonable satisfaction. It is important to realize, however, that the species intergrade completely, and that it will often be very difficult to determine for example, whether a strain belongs with *P. solitum* or *P. terrestre* on the one hand, or *P. terrestre* or *P. psittacinum* on the other. *Penicillium resticulosum* alone is unique in the dark reddish brown pigmentation produced in colony reverse. In considering the biochemical or physiological characteristics of any member of the *P. terrestre* series, it is believed preferable to regard such a strain as a representative of an abundant and variable series, possessing many characteristics in common, rather than as an exact representative of any particular species.

Penicillium psittacinum Thom, in The Penicillia, pp. 369–370. 1930.
Synonym: *Penicillium aureum* Corda, in Biourge Monogr., La Cellule **33:** 111–114, Col. Pl. I and Pl. I, fig. 2. 1923.

Colonies upon Czapek's solution agar growing fairly rapidly, attaining a diameter of 5 to 6 cm. in 12 to 14 days at 25°C. and forming a tough felt up to 1 mm. deep upon the surface of the agar, azonate to broadly but indistinctly zonate, and usually radiately wrinkled (fig. 117A), with broad white margin, conidial areas in the growing period showing a striking shade of parrot ("psittacinus") green near malachite green, deep turtle green or fluorite green (Ridgway, Pl. XXXII), becoming shades of olive gray in age and overgrown with a thin weft of aerial hyphae in which anastomosing ropes of hyphae are abundant; marginal areas typically show some funiculose hyphae during the growing period, with limited fasciculation sometimes evident in the deeper central areas; reverse colorless or in pale shades of yellowish orange; little or no exudate produced; odor pronounced, "earthy"; conidiophores with walls slightly roughened, about 4.0μ in diameter, arising either as short branches from trailing or ascending hyphae

mostly less than 50μ in length, or from the substratum and up to 200 to 250μ in length; penicilli asymmetric, commonly 25 to 30μ in length, occasionally 60μ, usually consisting of a main axis with or without one or more appressed branches, sometimes monoverticillate; conidial chains tangled, rarely exceeding 75μ in length; metulae irregularly produced, commonly in groups of 2 or 3, often at different levels, measuring 8 to 12μ by 2.2 to 3.3μ, occasionally up to 15μ in length; sterigmata 8 to 10μ by 2.5 to 3.0μ, closely packed, few in the verticil, often arising at different levels; conidia globose to subglobose, 3.5 to 5.5μ in diameter, variable in the same mount, with walls smooth or irregularly and finely roughened, yellow-green in mass.

Colonies on steep agar growing as described above but more closely wrinkled and much heavier sporing (fig. 117B), in color ranging from bright yellow-green shades (see above) in young sporulating areas through dull yellow-green to brownish olive in age; limited clear exudate produced; odor strong, "earthy", suggesting actinomycetes; penicilli more consistently asymmetric and larger but otherwise as on Czapek.

Colonies on malt extract agar 5.0 to 5.5 cm. in 12 days, comparatively thin, appearing velvety but with surface showing trailing hyphae or thin ropes of hyphae, heavily sporing, in bright yellow-green shades such as malachite and fluorite green (R., Pl. XXXII) with these colors persisting in age; no exudate produced; odor strong (see above); penicilli more abundantly produced, essentially duplicating those on steep agar but with conidiophores more conspicuously roughened.

Species description based primarily upon the type culture, NRRL 932 (Thom's No. 4733.12), received from Biourge as *Penicillium aureum* Corda, and approximated by strains occasionally isolated from soil. The two cultures received from the Centraalbureau as *P. psittacinum* Thom adequately represent the species although one of these now produces colonies that are predominantly sterile.

The correct placement of *Penicillium psittacinum* remains somewhat in doubt. In the type strain, the funiculose habit is usually evident and, for this reason, the species is assigned here. Thom (1930) noted that this culture, in deeper areas, commonly appeared fasciculate. In its basic coloration, NRRL 932 bears a striking resemblance to certain members of the *P. viridicatum* group, which are definitely fasciculate. The color changes for this strain on steep agar may likewise be significant, with colonies changing from bright yellow-green to brownish olive shades. In this latter character, it is suggestive not only of the *P. viridicatum* series but of some strains normally assigned to *P. ochraceum* as well. There is considerable evidence supporting the belief that *P. psittacinum*, *P. ochraceum* and the *P. viridicatum* series all belong to a single but extremely variable group in which color changes from yellow-greens to olive-browns represent a fundamental characteristic.

Penicillium terrestre Jensen, in Cornell University Exp. Sta. Bul. 315, pp. 486–487, fig. 122. 1912. Thom, The Penicillia, pp. 371–372. 1930.

Colonies upon Czapek's solution agar spreading broadly, attaining a diameter of 7.0 to 8.0 cm. in 12 to 14 days at room temperature, azonate in most strains, somewhat zonate in others, often deeply ridged in age, floccose-funiculose (fig. 117C), commonly 500μ to 1 to 2 mm. deep with ropiness readily observed under low magnifications, or occasionally thinning to a fraction of this depth and retaining only traces of ropiness, with margin broad, white during the growing period, passing into conidial zones

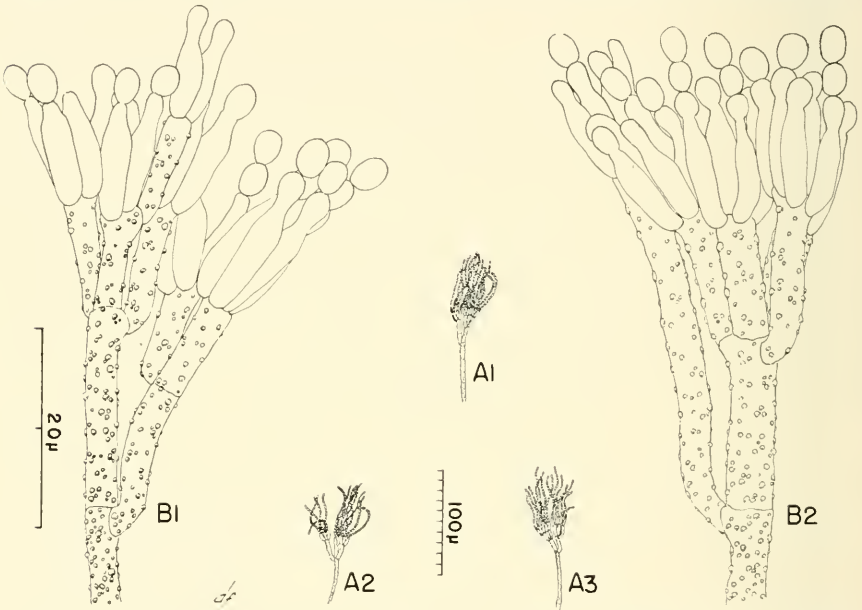


Fig. 116. *Penicillium terrestre* Jensen. A_1–A_3, Habit sketches of representative penicilli. B_1 and B_2, Penicilli showing details of cellular structure; conidiophores, branches and even metulae are characteristically roughened.

in shades of dull gray-green to slightly bluish green approximating mineral gray to celandine green (Ridgway, Pl. XLVII), then toward olive-gray and brown shades (R., Pl. LI) in old cultures; odor strong, like certain mushrooms; exudate limited in amount, clear; reverse mostly uncolored, or with dull yellow to orange shades sometimes evident in marginal zones; conidiophores about 3μ in diameter, arising from the substratum or as branches from aerial hyphae, varying greatly in length up to 400 to 500μ, with walls roughened as seen under oil immersion; penicilli comparatively large, commonly 40 to 50μ in length, bearing conidial chains at first in loose columns but becoming tangled in age (fig. 116A); asymmetric, usually

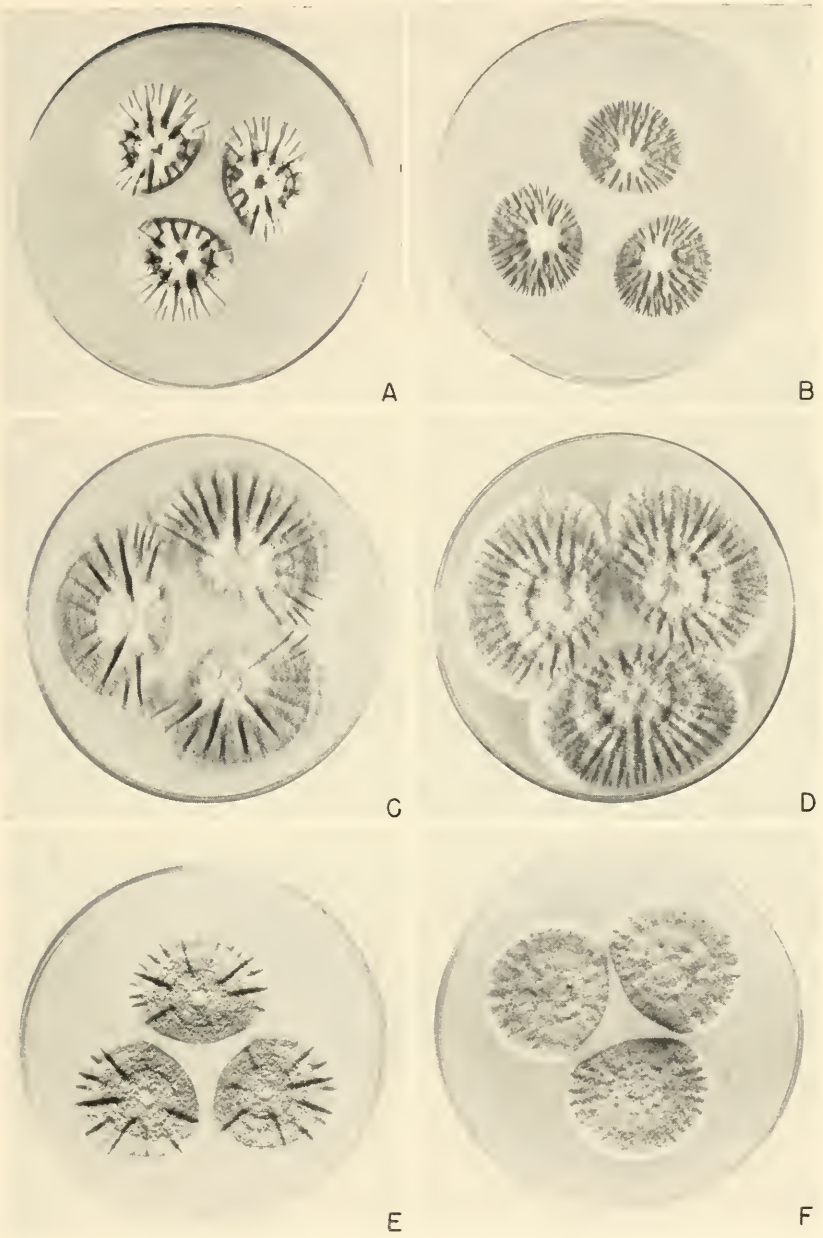


FIG. 117. *Penicillium terrestre* series. *A* and *B*, Two-week-old colonies of *P. psittacinum* Thom, NRRL 932, on Czapek and steep agars. *C* and *D*, *P. terrestre* Jensen, NRRL 934, as the preceding. *E* and *F*, *P. solitum* Westling, NRRL 937, as above.

consisting of the terminal axis and one, or occasionally two, more or less appressed branches bearing metulae and sterigmata, with branches and metulae commonly roughened (fig. 116B); branches variable in length, 15 to 30μ by 3.0 to 3.5μ; metulae usually in groups of 2 to 3 or more, 10 to 15μ by 3.0 to 3.5μ, with apices slightly inflated; sterigmata usually in clusters of 6 to 10, mostly 10 to 12μ by 2.5 to 3.0μ, occasionally up to 20μ in length, not infrequently arising at different levels; conidia extremely variable in size and shape, at first definitely elliptical, in age remaining so or becoming ovate or subglobose; mostly 3.5 to 4.0μ in long axis, occasionally up to 5.5 to 6.0μ, smooth-walled.

Colonies on steep agar similar to those on Czapek but generally more conspicuously floccose-funiculose (fig. 117D), usually heavier sporing and aging more rapidly, often becoming olive-gray to mouse gray (R., Pl. LI) in 12 to 14 days; penicilli essentially as described above.

Colonies on malt extract agar growing rapidly, usually covering the culture plate within 2 weeks, plane, loose-textured, with surface appearing cottony in some strains, almost velvety in others, with funiculose habit evident but not as pronounced as upon Czapek's solution or steep agars; exudate not produced; penicilli as described above but generally more compact, with elements usually shorter, and with conidiophores more conspicuously roughened.

Species description based upon strains NRRL 933 (Thom 5034.8) and NRRL 934 (Thom 5042.135), and duplicated by numerous additional strains isolated from soil and other natural sources. This species is abundant in nature and representative strains have been contributed by numerous collaborators. Professor Raistrick included several strains among the cultures sent from the Nobel Explosives Company in Ayreshire, Scotland; other strains have come from sugar beet studies at Logan, Utah and elsewhere.

Thom (1930, pp. 270–272) considered *Penicillium terrestre* Jensen to represent one aspect of a complex of floccose-funiculose forms which he grouped together as the *P. grisco-fulvum-terrestre* series. Careful re-evaluation of Biourge's discussion (1923, pp. 164–167) of *P. griseo-fulvum* Dierckx, together with a thorough re-examination of two sub-cultures of a strain derived from Biourge's culture and widely investigated under this name, now leads us to regard this species as probably representing some fasciculate form approximating *P. urticae* Bainier (see p. 536). *Penicillium terrestre*, now considered as probably quite separate from *P. griseo-fulvum*, shows marked variation in laboratory cultures. Different strains range in texture from floccose, through funiculose, to almost fasciculate, and vary in color from light yellow-green to rather dull blue- or gray-green.

Penicillium australicum Hann. (from Zach) has been listed among the species available from the Centraalbureau for many years. Thom, in 1936, received such a culture which upon careful study was found to represent a mixture of two species. One represented a ramigenous monoverticillate form which approximated *P. waksmani* Zaleski. This culture is maintained as NRRL 781 and still retains the characteristics noted for it in 1936. The other represented a faster growing and coarser fungus which showed a marked tendency to develop ropes or fascicles of aerial hyphae. Penicilli were rebranched and asymmetrical, conidiophore walls were somewhat roughened, and conidia were at first elliptical becoming subglobose in age. This strain was regarded as approximating *P. terrestre*. Unfortunately, it has been lost from our Collection.

Recently van Beyma has reviewed (1944–1945) the whole background of the name *Penicillium australicum*, and the possible origin of the strain sent to Baarn by Zach in 1928 under the name "*P. australicum* (Kap Labor) Hann." Van Beyma explains "Kap Labor" refers to Johan Olsen-Sopp's laboratory in Mjosen, Norway, whereas "Hann" is an abbreviation of Hannover and refers to Wehmer's Laboratory. The species as maintained at Baarn was thus without an author's name. Van Beyma concluded that there could be little question that *P. australicum* was isolated by Olsen-Sopp at the Kap Laboratory, but that he failed to publish a description. Van Beyma, therefore, proposed to assign the species to Olsen-Sopp and published a detailed description with Latin diagnosis under the name *P. australicum* (Olsen-Sopp) emend. v. Beyma (in Antonie v.Leeuwenhoek **10:** 53–56, fig. 10. 1944–1945).

In February 1946 two cultures were received from the Centraalbureau as *Penicillium australicum* and have been included in the present study. The first of these was labeled "*P. australicum* (Kap Lab.) Hann." listed as from Zach in 1928. The second represented an isolate by Rennerfelt from wood pulp received at Baarn in 1940. The former culture (which may represent the type) is a comparatively slow growing, slightly fasciculate form of dull blue-green color which in many respects approximates *P. puberulum* Bainier; conidiophores are conspicuously roughened and a strong moldy odor is produced on all substrata. The latter culture is less heavily sporing, tends to be deeply floccose with the development of considerable ropiness, conidiophores are slightly roughened on Czapek's agar and coarsely roughened on malt agar. The strain is regarded as probably best assigned to the *P. terrestre* series, although there is some evidence of fasciculation in colonies on malt agar.

Neither of these strains exhibits characteristics sufficiently marked to demand recognition of a separate species.

In view of the conflicting information that has accumulated, it is impossible for us to confidently assign or dispose of *Penicillium australicum*. It seems probable, however, that the name is generally understood to refer to molds approximating *P. terrestre* Jensen.

Penicillium solitum Westling, in Arkiv för Botanik **11:** 52, 65–67, figs. 3 and 47. 1911. Thom, The Penicillia, pp. 372–373. 1930.

Colonies on Czapek's solution agar growing fairly rapidly, attaining a diameter of 5.0 to 6.0 cm. in 12 to 14 days at 25°C., consisting of a tough basal felt with surface growth loose, floccose-funiculose, up to 1 mm. deep, more or less zonate, especially in marginal areas (fig. 117E); growing margin broad, whitish and usually showing definite ropiness, but in old

cultures becoming thin and almost velvety; heavily sporing throughout, with conidial structures arising from the substratum and from trailing hyphae or ropes of hyphae; in blue-green shades approximating artemisia green in young conidial areas to sage green and finally slate-olive in age (Ridgway, Pl. XLVII); exudate lacking or limited; odor sometimes pronounced, moldy, slightly fragrant; reverse colorless to drab shades; penicilli abundantly produced, comparatively large, appressed, measuring about 25 to 35μ in length but occasionally up to 50μ, consisting of the main axis and usually one branch, each bearing metulae and sterigmata, with conidial chains forming a loose tangled mass; conidiophores variable in length, up to 300 to 400μ by about 3.0 to 3.5μ when arising from the substratum, or shorter, commonly 100 to 200μ in length when borne on aerial hyphae, with walls smooth or very finely roughened; branches usually 10 to 20μ by 2.5 to 3.0μ; metulae mostly in groups of 2 to 4, 10 to 15μ by 2.5 to 3.0μ; sterigmata variable, commonly in groups of 5 to 10, 8 to 12μ by 2.0 to 2.5μ, not infrequently larger, commonly borne at different levels in the penicillus; conidia at first strongly elliptical, usually remaining so; about 3.5 to 4.5μ by 3.0 to 3.5μ, less commonly subglobose, varying greatly in the same mount, with individual spores up to 5.5μ in length, walls smooth, dark green in mass.

Colonies on steep agar essentially duplicating those on Czapek's solution agar, slightly deeper and with surface growth more conspicuously funiculose (fig. 117F); penicilli as described above.

Colonies on malt extract agar about 4.0 to 5.0 cm. in 12 to 14 days, up to 500μ deep, heavily sporing, with surface characterized by a loose network of trailing hyphae and ropes of hyphae; penicilli as on the above substrata.

Species description based upon NRRL 937 (Thom's No. 2546), received from Westling and presumably type; duplicated by numerous strains isolated from various substrata, particularly soil.

In its cultural appearance *Penicillium solitum* bears a certain resemblance to members of the *P. cyclopium* series. Unlike the latter forms, which usually show definite fasciculation, strains of *P. solitum* are generally conspicuously funiculose, but occasionally show evidence of true fascicles. Older colonies are commonly characterized by the development of limited flocculent, white, sterile overgrowths—a phenomenon which is not uncommonly encountered in *P. cyclopium*. It is probable that the two species are more closely related than their placement in separate groups would indicate. In describing *P. solitum*, Westling suggested comparison with *P. puberulum* Bainier. During our current study it has seemed increasingly probable that these species are in fact fairly closely related and that both should be considered as approaching *P. cyclopium* Westling. It seems

entirely possible that these may constitute a natural series in which colonies assume characteristics that are more apparent than fundamental, with *P. puberulum* producing colonies typically velvety but sometimes showing fasciculation; *P. cyclopium*, typically fasciculate but sometimes velvety; and *P. solitum*, typically funiculose but sometimes developing true fascicles or again appearing almost velvety and regularly producing conidial structures of the general habit and pattern of the other two species.

Penicillium resticulosum Birkinshaw, Raistrick, and Smith in Biochem. Jour. **36:** 829–835. 1942.

Authors' diagnosis:

"Colonies on Czapek agar spreading broadly, tenuous, at first white then pale bluish green with very broad funiculose margin, becoming fairly dark grey-green all over, floccose-funiculose, especially in outer areas, broadly and indistinctly zoned in old cultures; drops numerous during the growing period, small, pinkish; reverse quickly reddish brown to chestnut brown, shading to dull yellow near the margin; conidiophores long, mostly loosely aggregated in ropes rather than in true fascicles, smooth, 3–4μ in diameter; penicilli very compact, 2–3 verticillate, often with main axis bearing a terminal verticil of metulae and sterigmata and one or two appressed secondary branches bearing sterigmata at approximately the same level as the main axis, up to 100μ in total length; metulae somewhat clavate or definitely swollen at the tip, 14–19 by 3–3.5μ (4.5μ at tip); sterigmata 9–10μ x 2.2–3.0μ, widening upward then tapering abruptly to fine points; conidia cut off as more or less citriform segments, often resembling chains of oidia, subglobose when ripe, smooth, 3–4 x 2.8–3.2μ; conidial chains at first roughly parallel, in old cultures becoming much tangled.

"Cultures on wort agar remain sterile for several weeks if kept in the dark but well established colonies may be induced to form abundant spores by exposure for a few hours to diffuse light.

"Related to *Penicillium terrestre* Jensen and *P. solitum* Westling, but differing from both in texture of colonies and in colour.

"Found as a culture contaminant in the laboratory. The name chosen for the new species is descriptive of the colony texture".

The type strain, NRRL 2021, was received from George Smith, London School of Hygiene and Tropical Medicine, in November 1945 as L.S.H.T.M. Catalogue No. P-47.

Our notes on cultures of the type strain follow:

Author's description of colonies on Czapek's solution agar is carefully and accurately drawn (fig. 118A), and the general description of the penicillus is correct (fig. 118C), but metulae are somewhat shorter than reported, sterigmata are not particularly pointed, and conidia appear definitely elliptical when ripe.

Colonies on steep agar grow somewhat more rapidly than upon Czapek, completely covering the culture plate in 12 to 14 days (fig. 118B), and are generally more funiculose (fig. 118D).

Colonies on malt extract agar duplicate the authors' description for wort agar by remaining sterile for several weeks but, in our experience, fail to produce abundant conidial structures when placed in diffuse light.

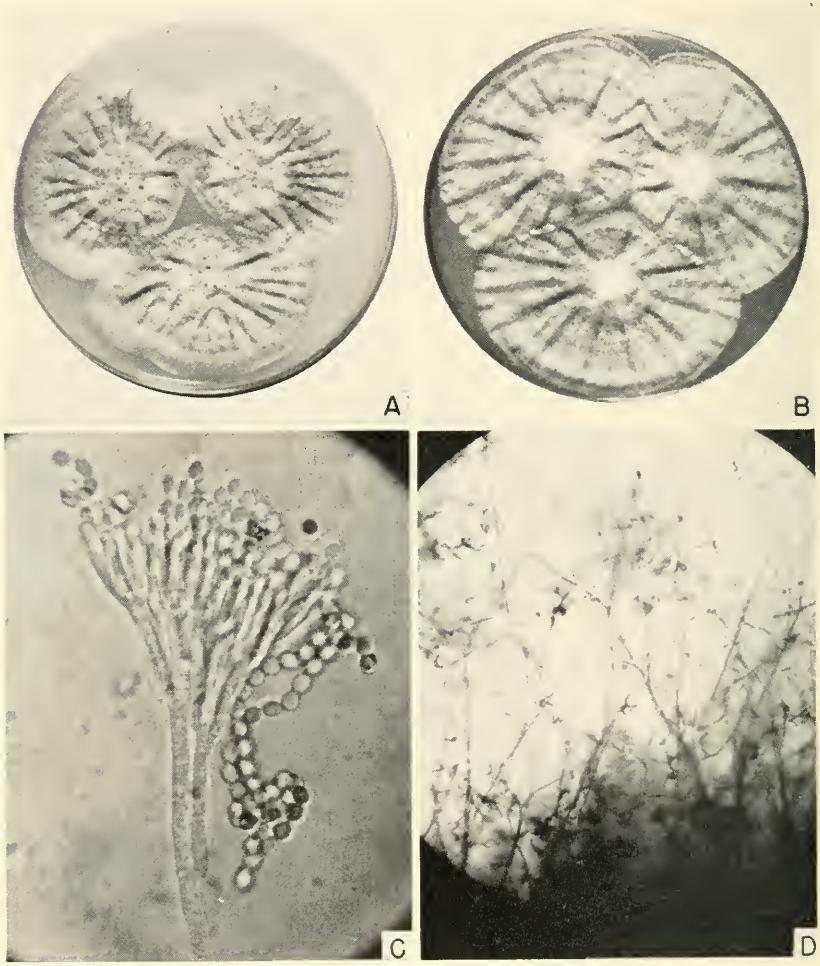


FIG. 118. *A* and *B*, *Penicillium resticulosum* Smith, NRRL 2021, on Czapek and steep agars. *C*, Detail of penicillus in the same strain, × 750. *D*, Low-power view of colony margin showing funiculose habit of aerial growth, × 70.

The species is easily distinguished, being characterized by its spreading, funiculose habit and its pronounced reddish brown pigmentation.

Occurrence and Significance

Penicillium terrestre Jensen and *P. solitum* Westling represent cosmopolitan fungi which may be encountered in almost any soil examined, or

upon almost any type of plant residue in the later stages of decomposition. Other members of the series, likewise regarded as primarily of soil origin, are apparently less abundantly distributed in nature. In no known case has a member of the series been isolated from a substrate that might be regarded as either specific or restrictive.

Birkinshaw and Raistrick (1936b) reported the production of a hitherto undescribed product of mold metabolism, terrestric acid, $C_{11}H_{14}O_4$, by three strains of *Penicillium terrestre*. The product is a colorless, crystalline acid showing many resemblances to the substituted tetronic acids earlier obtained from *P. charlesii* Smith by Clutterbuck, *et al.* (1934). It was shown to be an ethyl derivative of one of them, namely, carolic acid (see p. 252).

Atkinson (1942, 1943) reported the production of an antibiotic substance, designated "penicidin", from a mold which was subsequently submitted to us for identification and found to approximate *Penicillium terrestre*. In the following year, Atkinson, *et. al.*, (1944a) described a procedure for the purification and crystallization of penicidin; and in another paper (1944b) considered the antibacterial activity of additional molds belonging to the genera *Penicillium* and *Aspergillus*. Penicidin is now generally considered to represent the same substance as that to which other names, including claviformin, clavacin, and patulin, have been applied (see p. 537).

Penicillium solitum Westling was found to be a harmful organism in the leather industry by van Beyma (1936).

The production of oxalic acid by *Penicillium solitum* at different pH levels was studied by Jacquot (1938), the optimum being pH 7.5 to 7.8. Disaccharides, hexoses, and pentoses were successfully used as carbon sources.

Birkinshaw, Raistrick, and Smith (1942) reported *Penicillium resticulosum*, when grown on Czapek-Dox 5 percent glucose solution, to produce considerable quantities of the hitherto undescribed fumaryl-*dl*-alanine (fumaromono-*dl*-alanide) $C_7H_9O_5N$, m.p. 229° (decomp.), titrating as a dibasic acid. The product was synthesized from fumaryl chloride and *dl*-alanine and may be regarded as a simple peptide of fumaric acid and *dl*-alanine, into which constituents it is resolved upon acid hydrolysis. Metabolism solutions of *P. resticulosum* show considerable antibacterial activity. The antibacterial substance was isolated in crude form. Fumayrl-*dl*-alanine did not appear, however, to form an integral part of the molecule of the antibacterial substance. Coulthard, *et al.* (1945) reported the production of an antibiotic by *P. resticulosum* which they believed to approximate notatin, a product of *P. notatum* (see p. 376).

No biochemical or physiological studies are known to have been conducted on *Penicillium psittacinum* Thom.

Penicillium pallidum Series

Outstanding Characters

Colonies spreading, usually rather thin, with surface growth somewhat funiculose; conidia variable in color, white to cream, buff, light gray, or lavender to vinaceous—never developing true greens.

Conidiophores comparatively short, mostly arising from ropes of aerial hyphae; conspicuously septate, with walls of conidiophores, branches, and metulae closely and conspicuously roughened.

Penicilli usually comparatively narrow, with cellular elements tending to be closely appressed rather than divergent.

Sterigmata borne in compact clusters, closely parallel, comparatively thin, seldom exceeding 2.5μ in diameter, with walls often echinulate.

Conidia strongly elliptical to cylindrical, smooth-walled, often adherent in long chains in fluid mounts.

Series Key

A. Conidia white to cream colored.
   1. Conidial chains divergent, becoming tangled in age ..... *P. pallidum* Smith
   2 Conidial chains in well-defined columns ..... *P. putterillii* Thom

B. Conidia in light to dull gray shades ..... *P. namyslowskii* Zaleski

C. Conidia in light violet, lavender, or vinaceous shades. *P. lavendulum* Raper and Fennell

The species included here may or may not represent a natural series. All of them, however, possess certain marked characteristics in common which enable them to be considered together more satisfactorily than with any other recognized forms. Irrespective of their true relationship, the general pattern of the penicillus is much the same in all cases (fig. 119). This is likewise true of the character of conidiophore walls and the distinctive form of conidia.

The four species included may be separated as shown in the above key, and may be further characterized as follows: *Penicillium pallidum* Smith shows a complete lack of color in young conidial areas but tends to develop light cream shades in age. Conidiophores are usually quite short, conspicuously septate, and often arise from cellular elements in the parent hyphae that are strongly suggestive of the foot-cells of *Aspergillus.* The same is seen to a lesser degree in other members of the series. *Penicillium putterillii* Thom, as originally described, differs from the above primarily in producing colonies in darker shades, approaching avellaneous. *Penicillium namyslowskii* Zaleski is distinguished by its very sparse, spreading colonies on Czapek agar, coupled with the production of dirty white to very light gray conidial masses and the development of a very strong penetrating earthy odor on all substrata. *Penicillium lavendulum* Raper and

Fennell is distinguished by its heavier spore production, its larger penicilli, and especially the striking color of its conidial areas which range from light bluish violet through lavender to deep vinaceous depending upon the substratum.

Thom, as reported by George Smith in his discussion of *Penicillium pallidum* (1933), has suggested that the origin of conidiophores from foot-cell-like initials may necessitate the recognition of a separate section within the genus *Penicillium* to include these forms, together with *P. varians* Smith (see p. 625). The penicillus of the latter species is, however, typi-

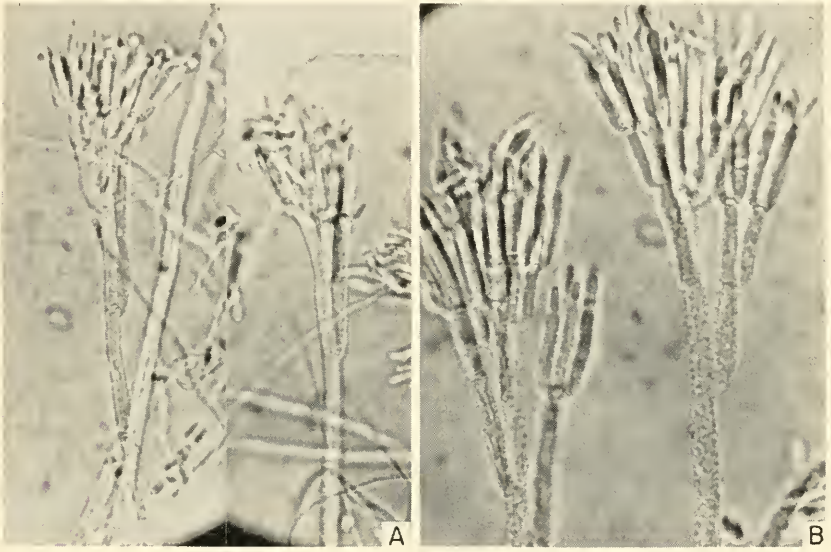


FIG. 119. *A*, Penicilli of *Penicillium pallidum* Smith, NRRL 2037, × 750. *B*, Penicilli of *P. lavendulum* Raper and Fennell, NRRL 2146, × 900. Note the conspicuously roughened conidiophores, the closely parallel sterigmata and the cylindrical to strongly elliptical conidia that characterize both species.

cally biverticillate and symmetrical. In this, as in other characters, including colorat on and the lanceolate pattern of its sterigmata, *P. varians* seems to be clearly related to the *P. funiculosum* series of the Biverticillata-Symmetrica. The examination of additional Penicillia showing conidiophores of similar origin may subsequently necessitate a revision of our current views on relationships and eventually form the bases of a somewhat altered classification. For the present, however, we believe it is most practicable, in these cases as in all others, to base primary separation upon the pattern of the penicillus, and to then assign different strains and species according to whatever secondary groupings are dictated by colony texture and other characteristics regarded as of secondary importance.

FIG. 120. *Penicillium pallidum* series. *A*, *B*, and *C*, Two-week-old colonies of *P. pallidum* Smith, NRRL 2037, on Czapek, steep, and malt agars, respectively. *D*, *E*, and *F*, *P. lavendulum* Raper and Fennell, NRRL 2146, as the preceding.

Penicillium pallidum Smith, in Bot. Mycol. Soc. Trans. **18:** 88–89, Pl. IV, figs. 1 and 2. 1933.

Colonies on Czapek's solution agar spreading, attaining a diameter of 6.5 to 7.0 cm. in 2 weeks at room temperature, radially furrowed, somewhat zonate, when young consisting of a white, tough, submerged, mycelial growth which later gives rise to a sparse development of conidiophores and short funiculose tufts or ropes of aerial hyphae bearing conidiophores (fig. 120A), becoming cream colored in age; no exudate; odor evident, not pronounced; reverse uncolored to light cream; penicilli mostly asymmetric biverticillate (fig. 119A), 35 to 55μ in total length; bearing conidial chains at first roughly parallel, becoming tangled in age; conidiophores arising from creeping hyphae or from definite ropes of hyphae, many originating from clearly differentiated foot-cells as found in *Aspergillus*, others terminal on long trailing hyphae which gradually enlarge to the diameter of the conidiophores, tapering slightly towards the penicillus, definitely roughened (fig. 119A); metulae rough, 11 to 14μ by 2.0 to 2.5μ in diameter; sterigmata finely spinulose, bluntly pointed, 11 to 12μ by 2.0μ; conidia elongate 3.2 to 4.0μ by 1.5 to 2.2μ, smooth-walled.

Colonies on steep agar growing slightly less rapidly than on Czapek, more closely wrinkled radially, producing more surface growth with funicles or ropes more prominent (fig. 120B), odor more pronounced; reverse in dull, light buff shades; otherwise as on Czapek agar.

Colonies on malt extract agar attaining a diameter of 5.0 to 5.5 cm. in 2 weeks at room temperature, white, producing abundant floccose-funiculose hyphae in definite ropes up to 6 mm. long over the entire colony surface (fig. 120C); reverse in slightly darker buff shades than on steep agar; odor strong, suggesting sour cream; microscopically duplicates the description on Czapek agar.

Species description based upon the author's diagnosis and upon our notes on Smith's type strain (Catalogue No. 76) received by Thom in 1931. The culture was subsequently lost from his collection but has been returned to us for the present study by Dr. R. St. John-Brooks, National Collection of Type Cultures, London, and is now maintained as NRRL 2037. The type was obtained originally from samples of yarn showing no sign of mildew. A second representative strain received from the Centraalbureau in May 1946 was labeled: "from elm beetle, 1932". The species appears to be fairly uncommon.

Penicillium putterillii Thom, in The Penicillia, pp. 368–369. 1930.

Colonies on Czapek's solution agar attaining a diameter of 4.0 to 5.0 cm. in 12 to 14 days at 25°C., forming a tough, close-textured basal felt at

first largely submerged and appearing wet, subsequently developing abundant conidial structures in marginal areas, white to buff shades (Ridgway, Pl. XL), radiately wrinkled in quadrants, with growing margin 1 to 2 mm. wide, partially submerged, strongly funiculose, and with ropiness evident but less conspicuous in older colony areas; no exudate produced; odor lacking or indefinite; reverse uncolored to yellowish cream; penicilli comparatively small, usually consisting of a terminal verticil of 2, 3, or more metulae bearing clusters of sterigmata and conidia in fairly well-defined columns; conidiophores mostly arising from ropes of hyphae, usually less than 100μ by 4.0 to 5.0μ, with walls conspicuously roughened; metulae rough-walled, 8 to 12μ by 2.5 to 3.0μ bearing closely crowded sterigmata in groups of 5 to 10 or 12, about 6, to 8μ by 2.0μ with walls sometimes definitely roughened; conidia cylindrical to elliptical 4.0 to 5.0μ by 2.0 to 3.0μ, smooth-walled, colorless in mass.

Colonies on steep agar growing more rapidly than above, looser in texture, with surface growth conspicuously funiculose throughout the entire colony area, sporulating more abundantly, with penicilli as described above.

Colonies on malt extract agar more restricted, 3.0 to 4.0 cm. in 12 to 14 days at 25°C., plane, with surface appearing slightly granular and with funiculose habit reduced or almost lacking; penicilli abundantly produced, borne on conidiophores arising primarily from the substratum, generally somewhat larger than above, with sterigmata commonly 10μ in length and producing fairly well-defined columns of conidia up to 100 to 200μ long.

The species was described by Thom, in 1930, from a culture (his No. 4658.34) sent to him by F. M. Putterill, Cape Town, South Africa. This culture was quickly lost from his collection. A strain sent to us by the Centraalbureau in May 1946, isolated by Neill from lumber in New Zealand, has been examined in the present study. The latter culture, maintained in our Collection as NRRL 2024, apparently differs from the original only in producing conidia that are more consistently white, hence approaches *Penicillium pallidum* Smith in general appearance and coloration.

Penicillium namyslowskii Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B., pp. 479–480, Taf. 52. 1927; Thom, The Penicillia, pp. 484–485. 1930.

Colonies on Czapek's solution agar spreading rather broadly, up to 3.5 to 4.0 cm. in 2 weeks, very thin, with vegetative mycelium wholly submerged and hardly evident except when the culture is viewed toward the light, producing limited conidial structures, mostly near the colony center,

less abundant in marginal areas, conidial heads colorless or dirty white to very light gray; exudate limited in amount, adherent to the hyphae and conidiophores; odor strong, penetrating, earthy; reverse uncolored; conidial structures sparsely produced, generally arising from submerged hyphae; conidiophores erect, comparatively coarse, from 60 to 125μ by 4.0 to 5.0μ with walls conspicuously and coarsely roughened; penicilli typically biverticillate, commonly showing a terminal cluster of metulae but sometimes branched, usually asymmetric in pattern; metulae in groups of 2 to 4 or 5, from 10 to 13μ by 4.0 to 5.0μ with walls conspicuously roughened; sterigmata few in the verticil, closely compacted, usually parallel, 7 to 9μ by 2.2 to 2.8μ, rough-walled, terminating rather abruptly; conidia at first strongly elliptical to capsule-shaped or almost rectangular, 2.8 to 3.3μ by 2.0 to 2.5μ, smooth-walled, characteristically forming irregular slimy masses in which individual conidia commonly swell, become rounded, and germinate.

Colonies on steep agar spreading broadly, 7 to 8 cm. in 2 weeks, closely wrinkled in a cerebriform pattern, thin, close-textured, appearing wet, dirty white to light gray becoming dull light brown in age, conidial structures sparsely produced at 2 weeks, fairly abundant at 4 weeks; exudate lacking; odor strong, penetrating; reverse uncolored to light gray; penicilli as described above but commonly forming irregular columns of enslimed conidia up to 75 or 100μ in length.

Colonies on malt agar as on steep agar except marginal areas less closely wrinkled; penicilli as described above.

Species description based upon NRRL 1070, received in 1928 from the Centraalbureau as Zaleski's type and discussed by Thom in his Monograph (1930) as his No. 5010.16.

The above description is in fairly close agreement with Zaleski's original diagnosis except for the conspicuously roughened conidiophores (Zaleski reported and illustrated all walls as smooth). In studying the above strain, received as Zaleski's type, Thom (1930, p. 485) reported conidiophore walls as rough, and penicilli as either symmetrical or asymmetrical. The culture now in our possession retains the characters observed by Thom and is believed to represent Zaleski's original isolate despite the reported differences in the character of conidiophore walls.

Thom placed this species in the Biverticillata-Symmetrica adjacent to *Penicillium tardum*, largely because of its limited growth upon Czapek's solution agar. Such a relationship seemed to be further indicated by the biverticillate and sometimes symmetrical pattern of its penicilli. Careful re-examination of the type culture, and comparison with recognized members of the *P. tardum* series, has led us to question this relationship. The

presence of asymmetric penicilli and non-lanceolate sterigmata, together with the production of strong earthy odors on different substrata, suggests other relationships.

The very rough walls of conidiophores, metulae, and even sterigmata found in NRRL 1070 are characteristic of the *Penicillium pallidum* series in the Funiculosa. Conidia are in dirty white to dull light gray shades, rather than white to cream colored as in most other members of this series. Furthermore, this species grows thinly upon all substrata, particularly Czapek, and the funiculose character usually associated with members of the *P. pallidum* series, to which it is assigned, is somewhat limited but clearly evident when the colony surface is viewed under low magnifications. We believe the species is more closely allied to other members of the *P. pallidum* series than to any other recognized forms.

Penicillium lavendulum Raper and Fennell, in Mycologia. **40**: 530–533, fig. 8. 1948.

Colonies on Czapek's solution agar (Col. Pl. VII) spreading broadly, attaining a diameter of 5.0 to 6.0 cm. in 12 to 14 days, plane or nearly so, azonate, comparatively thin with vegetative mycelium largely submerged and with surface growth consisting of a loose weft of flocculent to cottony hyphae, showing some ropiness mostly in marginal to submarginal areas, sporulating most abundantly in central areas (fig. 120D), approximating dark grayish lavender to Ramier blue (Ridgway, Pl. XLIII), thinning through lighter shades to uncolored at the colony margin; exudate limited, in small drops, colorless; odor slight; reverse uncolored to light purple; penicilli variable in size, with conidial chains up to 100μ in length, loosely parallel, tangled or matted; conidiophores sometimes arising from the substratum, but borne primarily as branches from aerial hyphae, commonly 100 to 150μ in length by 3.0 to 3.5μ in diameter, sometimes shorter, septate, with walls closely echinulate; penicilli asymmetrical, irregularly once- or twice-branched (fig. 119B), with metulae commonly arising at different levels within the penicillus; branches mostly 2.5 to 3.0μ in diameter, varying greatly in length up to 15 to 20μ; metulae mostly 8 to 10μ by 2.5 to 3.0μ, often roughened (fig. 119B); sterigmata in compact clusters, closely parallel, 7 to 9μ by 2.0 to 2.2μ, with apices slightly narrowed but lacking well-defined conidium-bearing tubes, commonly rough-walled; conidia strongly elliptical (fig. 119B), from 3.0 to 4.5μ by 2.0 to 3.0μ, with walls smooth and comparatively heavy, tending to adhere into chains in fluid mounts.

Colonies on steep agar growing as on Czapek but somewhat deeper and generally heavier sporing (fig. 120E), predominantly dark grayish lavender but often appearing somewhat mottled from irregular spore production in

submarginal areas; reverse in purple-vinaceous shades, thinning toward the margin; penicilli as described above but commonly larger, with cellular elements somewhat longer; conidia more strongly elliptical, capsule-shaped.

Colonies on malt extract agar broadly spreading, plane, like the preceding in pattern and texture but usually heavier sporing, with massed penicilli forming crusts of conidia up to 400 or 500μ deep (fig. 120F), developing reddish tints to form shades near deep purplish vinaceous to dull Indian purple (R., Pl. XLIV); reverse in dull to deep purple-vinaceous shades; conidiophores arising mainly from the substratum; penicilli as described above but commonly larger and more complex, up to 50 or 60μ in length, with walls of conidiophores, branches, and metulae conspicuously roughened; conidia strongly elliptical or capsule-shaped, 4.0 to 4.5 by 2.0 to 2.5μ, smooth-walled.

Species descriptions based upon NRRL 2146, as type, isolated in July 1947 as a laboratory contaminant. The binomial *Penicillium lavendulum* was based upon the characteristic coloring of the species upon Czapek and steep agars.

The correct placement of the species remains somewhat in doubt since it typically develops more complexly branched penicilli than other species belonging to the *Penicillium pallidum* series. The roughened conidiophores and cellular elements of the penicilli, its strongly elliptical to capsule-shaped conidia, and the funiculose character of its colonies on Czapek's agar, however, seem to relate it to the *P. pallidum* series more closely than to any other recognized group. Furthermore, colonies on malt agar occasionally develop limited sectors or overgrowths characterized by almost colorless conidia, and isolations made from such areas commonly show little or no pigmentation of conidia. In gross appearance these substrains often strongly suggest such species as *P. putterillii* and *P. pallidum*.

Bainier, in 1906 (Bul. Soc. Mycol. France **22:** 207, Pl. XI, figs. 7–13) described a species, *Penicillium rubescens*, characterized by strongly elliptical conidia with fruiting areas in reddish or rusty shades. Penicilli were described and figured as complex and repeatedly branched, with cellular elements coarse and very short. Were it not for such marked differences in the general patterns of the penicilli of the two forms, our culture might possibly be regarded as representing Bainier's species.

Occurrence and Significance

Members of this series are apparently uncommon in nature. In no case has a species been reported frequently, and one species, *Penicillium lavendulum*, is known only as the type. Smith (1933) isolated *P. pallidum* originally from yarn, but observed no evidence of mildew. The species has

been re-isolated at Baarn from an elm-beetle but without report of significance. *Penicillium namyslowskii* is known only as Zaleski's type from Polish soil, although other strains suggestive of it have occasionally been seen. *Penicillium putterillii* was originally isolated in fruit storage studies in South Africa, while the strain received from Baarn under this name was isolated by Neill from wood in New Zealand.

No biochemical or physiological study of any member of this series is known to us.

Chapter XII

ASYMMETRICA

Sub-section: FASCICULATA

Members of the Fasciculata are characterized by the aggregation of part or all of the conidiophores into erect bundles or fascicles. Appearances range from colonies showing rudimentary bundles of conidiophores giving a granular, tufted or rough appearance to the white growing margin, to others with definite coremia mixed with simple conidiophores, to a few species in which all or nearly all of the conidiophores are aggregated into more or less sharply marked coremia. Gradually we have come to believe that descriptions in which the colony is reported as "granular," "mealy," or "tufted," as well as the variations upon such words as coremia, coremiform, flabelliform, and Isariaeform, are all more or less descriptive of the appearance given to the surface of the growing colony by the fasciculation of its conidiophores.

Doubts regarding allocation of species are certain to arise since questionable forms are encountered in this as in every other group of cosmopolitan species. Some series within the Fasciculata tend to merge imperceptibly into one another; furthermore, no sharp lines of demarcation exist between this sub-section and the Velutina, the Lanata, or the Funiculosa. Because of this variability and the intergradation of forms, certain arbitrary assignments have to be made. These are based upon what seems to be the consensus of all useful diagnostic characteristics. The Fasciculata includes a great multitude of strains differing in rate and habit of growth, and in color of conidial areas and colony reverse. Despite this, some lines of division seem to be more or less stable, and to separate fairly well-defined series. Within these series, certain described forms constitute centers for the recognition of species, or aggregates of strains that possess common morphology and show a general agreement in physiological activity, but often differ in shade of color and in the quantity of mycelium and spores produced.

Some cultures have been maintained in the laboratory for many years without substantial change. Other cultures vary markedly, and after a few successive transfers may leave the worker doubtful of the continuity of the strain which he seeks to maintain pure.

As a working basis for separation, we are arranging the species assigned to the group into nine series, in each case centered about the member-species which is most commonly encountered or is the most characteristic. In most of these series the aerial growth on Czapek's solution agar consists

of a mixture of simple conidiophores and fascicles of conidiophores, with simple conidiophores usually predominating (fig. 121A). In the series typified by *Penicillium granulatum* Bainier, however, fascicles of conidiophores are very prominent and often dominate the colony appearance

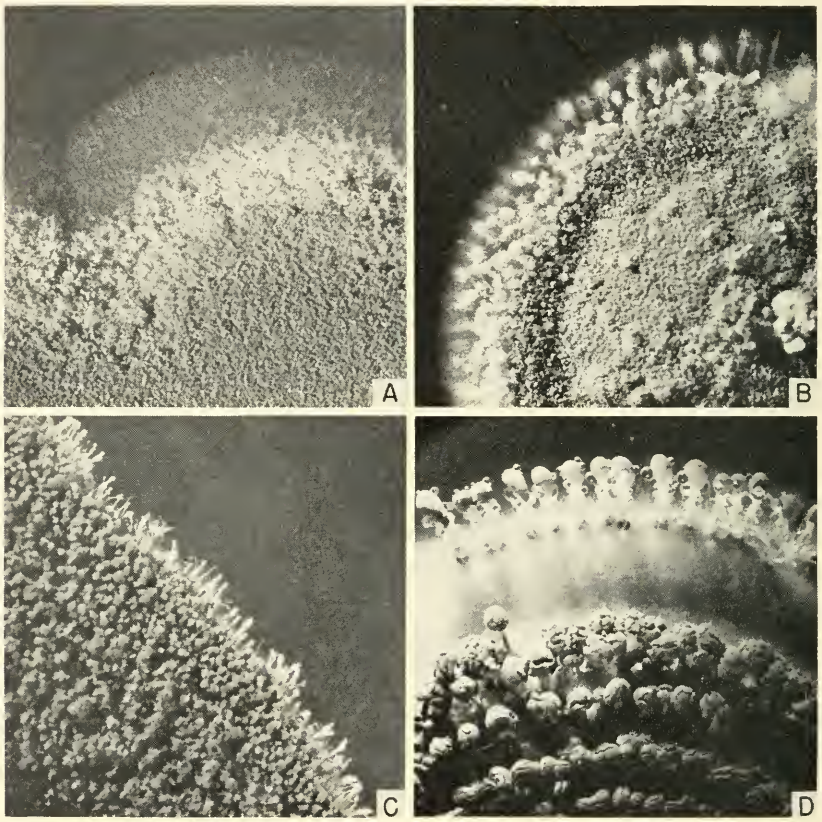


FIG. 121. The Fasciculata. *A–D*, Species showing progressive stages in fasciculation from lightly tufted to strongly coremiform. *A*, *Penicillium cyclopium* Westling, NRRL 1899, × 5. *B*, *P. italicum* Wehmer, NRRL 1293, × 10. *C*, *P. granulatum* Bainier, NRRL 2036, × 5. *D*, *P. claviforme* Bainier, NRRL 2149, × 3.

(fig. 121C), although single conidiophores are also regularly found. In the series typified by *P. claviforme* Bainier, conidiophores are almost entirely aggregated into large coremia (fig. 121D), often ranging from 3 to 5 mm. or more high by 1 mm. or more wide. These latter organisms have often been referred to the genus *Coremium*. Among the forms where simple conidiophores generally predominate, separation into series is based primarily upon growth and color characteristics, with emphasis in some cases placed upon their natural habitat where this is more or less diagnostic.

In all members of the group the penicilli are asymmetric, comparatively large, and usually show one or more branches in addition to the main axis, with each such major element terminated successively by verticils of metulae, sterigmata, and long, usually divergent chains of conidia. Conidiophores typically arise directly from the substratum, are usually fairly long and comparatively coarse; they may be either rough- or smooth-walled. Colonies of many species produce a strong odor which is generally diagnosed as moldy or earthy, although in some cases as aromatic.

Key to the Fasciculata

I. Species producing sclerotia.

Page

A. Fasciculation or aggregation of conidiophores usually encountered; penicilli typically branched below the level of the metulae.

1. Sclerotia abundantly produced at 25–30°C., less abundantly at lower temperatures; conidiophore walls roughened.....*P. gladioli* series 471

P. gladioli Machacek 471

2. Sclerotia or perithecia produced in occasional strains or under special conditions; conidiophore walls smooth.....*P. italicum* Wehmer 526

B Fasciculation not encountered; penicilli usually showing a single verticil of metulae.....*P. raistrickii* series

(see the Divaricata, p. 275)

II. Species not producing sclerotia.

A. Colonies with simple conidiophores and fascicles intermixed, but with simple conidiophores usually predominating.

1. Colonies lacking true green colors in areas of ripe conidia.

P. ochraceum series 475

a. Conidial areas in yellowish olive, buffy olive or buffy brown shades.

P. ochraceum (Bainier) Thom 477

b. Conidial areas in lighter shades near sandy brown or pinkish buff.

P. carneo-lutescens Smith 479

c. Conidial areas colorless or in light cream shades.

Color mutants of *P. urticae* and other species 536

2. Colonies characteristically developing yellow-green, blue-green, or gray-green shades in areas of ripe conidia.

a. Colonies typically in bright yellow-green to dark yellow-green shades; conidiophores usually rough-walled.*P. viridicatum* series 481

1′. Conidial areas showing bright yellow-green shades, at least when young.

aa. Colonies remaining bright yellow-green in age or tardily becoming light brown; odor pronounced.

P. viridicatum Westling 482

bb. Colonies at first bright yellow-green but quickly becoming dull and often showing vinaceous shades in older areas; odor very strong.....*P. olivino-viride* Biourge 487

2′. Conidial areas quickly developing dark yellow-green shades.

P. palitans Westling 488

b. Colonies typically in blue-green (aeruginous) shades, with the blue

element predominant or at least usually clearly evident; conidiophores smooth or rough-walled..... *P. cyclopium* series 490

1′. Colonies in dull blue-green shades, mostly azonate or indistinctly zonate; conidiophores on Czapek agar generally roughened; conidia usually subglobose.

aa. Colonies with surface usually granular or tufted and with definite fascicles appearing at least in the marginal areas.

1″. Conidia smooth or delicately roughened.

P. cyclopium Westling 493

2″. Conidia rough-walled and globose or nearly so.

P. cyclopium West. var. *echinulatum* n. var. 497

bb. Colonies with fasciculation often reduced and with sporulating surfaces often appearing velvety or lanose.

P. puberulum Bainier 497

2′. Colonies usually in brighter blue-green shades; often narrowly zonate; conidiophores on Czapek agar generally smooth; conidia usually elliptical.

aa. Colonies fairly rapidly spreading, heavily sporing on malt agar.....*P. martensii* Biourge 500

bb. Colonies more restricted, non-sporulating on malt agar.

P. aurantio-virens Biourge 503

c. Colonies typically in dull yellow-green, gray-green, or glaucous shades; conidiophores smooth or rough; responsible for a destructive rot of pomaceous fruits.....*P. expansum* series 508

1′. Conidiophores comparatively long, often up to 500μ or more in length, with walls smooth or finely roughened; conidia abundant but usually not forming definite crusts.

P. expansum Link 512

2′. Conidiophores usually shorter, with walls conspicuously roughened; conidia often forming definite crusts which break away when the culture tube or dish is tapped....*P. crustosum* Thom 516

d. Colonies typically in pale to dull gray-green or gray shades, seldom in yellow-greens; conidiophores typically smooth-walled.

1′. Colonies growing restrictedly upon Czapek but spreading broadly upon steep and malt agars; sterigmata 8–12μ long, few in the verticil; conidia strongly elliptical; responsible for a soft rot of citrus fruits.....*P. italicum* series 523

P. italicum Wehmer 526

2′. Colonies growing rather restrictedly upon Czapek, steep and malt agars; sterigmata 4.5 to 6.0μ in length, numerous and crowded in the verticil; conidia broadly elliptical.

P. urticae series 531

P. urticae Bainier 534

B. Colonies with most of the conidiophores arranged in fascicles or in definite coremia.

1. Fascicles or coremia predominating, but interspersed with abundant simple conidiophores; conidiophore walls roughened.

P. granulatum series 539

a. Conidia globose to subglobose; colonies 1.0–2.0 mm. deep; conidial areas in yellow-green to dark yellow-green shades; odor usually not pronounced.....*P. corymbiferum* Westling 540

b. Conidia elliptical; colonies 2.0–4.0 mm. deep; in pale blue-green to glaucous shades; odor pronounced, aromatic. *P. granulatum* Bainier 544

2. Coremia prominent, with simple conidiophores few in number or lacking; conidiophore walls smooth..... *P. claviforme* series 548

a. Coremia typically club-shaped and showing clear differentiation into a compact fibrous stalk and an expanded "sporehead" composed of massed and interwoven penicilli.... *P. claviforme* Bainier 549

b. Coremia typically loose in texture (Isaria-like), often not clearly differentiated into stalk and "sporehead"; commonly appearing feathery with penicilli usually separate. *P. clavigerum* Demelius 553

Penicillium gladioli Series

Outstanding Characters

Sclerotia characteristically produced, varying in number in different isolates and depending upon environmental factors, particularly temperature; usually produced abundantly at temperatures of 25°C. and above, scantily at 15°C. and below.

Conidiophores arising primarily from the substratum, mostly as independent structures but often more or less aggregated into definite fascicles, the latter usually more pronounced at low incubation temperatures; with walls roughened.

Penicilli comparatively large, usually consisting of one or two branches in addition to the main axis and each major element terminating in metulae bearing sterigmatic cells and conidia in tangled to loosely parallel chains.

Commonly producing a storage rot in gladiolus corms.

This series is represented by a single well-defined species, *Penicillium gladioli* Machacek. Considerable variation is encountered among strains newly isolated, and cultures long maintained in culture often tend to become more floccose and to produce relatively fewer sclerotia. Members of the series are differentiated from the sclerotium-forming species of the *P. raistrickii* series primarily upon the bases of their larger and looser conidial structures and the normal development of definite fasciculation of conidiophores.

Strains of *Penicillium italicum* Wehmer (see p. 526), when freshly isolated, sometimes produce sclerotia and might conceivably be confused with members of this series. These, however, differ in the substrata from which they are regularly obtained (*i.e.* citrus fruit), they produce abundant conidia at room temperature and usually show a more consistent and marked fasciculation, conidiophores are smooth-walled, and conidia are usually larger and more conspicuously elliptical.

Penicillium gladioli Machacek, in Quebec Soc. for the Protection of Plants Ann. Rpt. **19:** (1926–27): 77–86. 1928. Independently published

under the same specific name by McCulloch and Thom, Science N.S. **67:** 216–217. 1928. See also, McCulloch and Thom in Jour. Agr. Res. **36:** 217–224, Pl. I. 1928; Thom, The Penicillia, pp. 381–383, fig. 58. 1930.

Colonies upon Czapek's solution agar differing in habit when grown at different incubation temperatures: At temperatures above 25°C., producing abundant sclerotia with conidiophores generally few and inconspicuous; at 15°C. or lower, showing abundant green conidial areas with delayed or partially suppressed sclerotium formation. Upon Czapek's solution agar at 24°C. producing somewhat restricted colonies consisting of a fairly tough basal felt, with central area commonly raised and more or less floccose, and with marginal area radially and irregularly furrowed (fig. 122A); sclerotia normally appearing about the fifth or sixth day and developing in successive concentric zones in some strains or as sectors or localized areas in others, and giving the characteristic appearance of the species, varying greatly in size, commonly 150 to 300μ but sometimes up to 550μ in diameter, at first cream to light pinkish tan, in age becoming tan or very pale brown, smooth, and composed of thick-walled cells 8 to 12μ in diameter, retaining their vitality several months (fig. 122C); odor none; drops of orange-yellow fluid often more or less conspicuous; reverse at first uncolored or yellowish, eventually light pinkish cinnamon; conidiophores generally few, scattered, and inconspicuous among the sclerotia in strains newly isolated, in older stock cultures more abundant and commonly arising from within the floccose felt, often very long (up to 2 mm.) and about 3.0 to 3.6μ in diameter, with walls more or less roughened, later developing in more or less conspicuous tufts, fascicles, or complex branching coremia in the center of the colony and definitely green (bluish gray-green); penicilli usually consisting of the main axes of the conidiophores with or without one or two branches (fig. 122D), 15 to 25μ by 2.5 to 3.0μ, bearing few metulae 10 to 12μ long; sterigmata 10 to 12μ by 2.0 to 2.5μ, with tapering rather than acute points, in verticils of 4 to 8; conidia subglobose to elliptical, smooth, hyaline, 2.8 to 3.6μ by 2.5 to 3.0μ, often adhering in long chains in fluid mounts, more or less parallel, tangled as seen in the penicillus.

Colonies on Czapek's solution agar when grown at 14° to 15°C. producing abundant mycelium and conidial areas light dull glaucous blue, glaucous blue, or greenish glaucous blue (Ridgway, Pl. XLII) to the very margin of the colonies; sclerotium formation delayed and reduced, not dominating the growth; conidiophores partly simple, partly aggregated into coremia, tending to be longer and coarser, commonly 3μ to 4.5μ in diameter, with walls pitted or roughened; penicilli coarser, more complexly

branched, and with larger verticils of sterigmata than in the colonies grown at higher temperature, but with conidia not differing from the above.

Colonies on steep agar at 24°C. growing more rapidly than on Czapek but essentially similar in pattern and texture. Sclerotia abundant, gener-

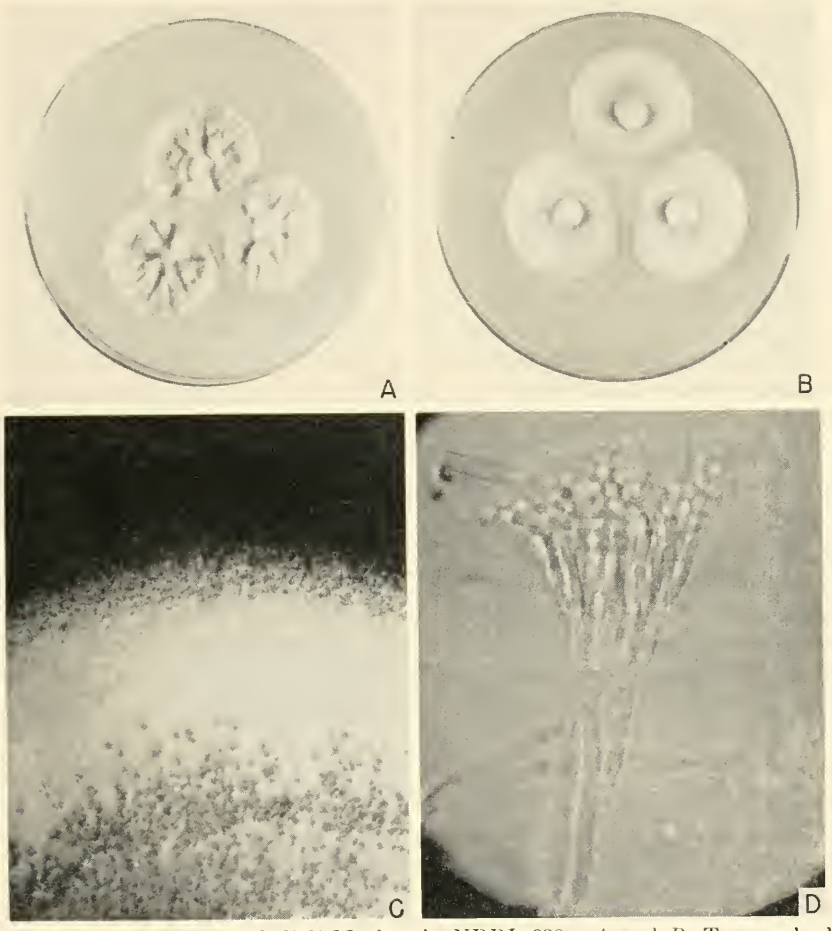


FIG. 122. *Penicillium gladioli* Machacek, NRRL 938. *A* and *B*, Two-week old colonies on Czapek and malt agars incubated at 25°C. *C*, Colony margin showing abundant sclerotia, malt agar, × 5. *D*, Detail of penicillus, × 750.

ally in a layer adjacent to the agar surface, commonly overgrown with loose, floccose, vegetative growth, conidial structures abundant, arising from the substratum or from within the mycelial mass; penicilli similar to those on Czapek; sclerotia as described above.

Colonies on malt agar at 24°C. consisting of a thin, more or less discontinuous felt bearing abundant sclerotia which generally dominate the colony pattern (fig. 122B), conidial structures few in number, scattered, and generally appearing less complex, with elements thinner than on Czapek but otherwise as described above. Conidial structures abundantly produced at lower incubation temperatures.

The species is often found as a cause of decay in gladiolus corms and is occasionally isolated from soil.

Species description based primarily on strain NRRL 939 received from the Thom Collection as No. 4885, isolated originally by McCulloch and regarded by Thom (1930) as the species type; duplicated by NRRL 938, from the Thom Collection as No. 5034.65, received originally from Dr. Birkinshaw in England; duplicated also by a strain received from the Centraalbureau in April 1946 as an isolate from gladiolus corms in 1941. A second strain received from Baarn as Machacek's culture, and presumably type, differs from the above in producing more restricted colonies that are more conspicuously floccose and produce comparatively few sclerotia, even on malt agar.

This species appears to have been isolated during the same year by J. E. Machacek at MacDonald College, Quebec, O. H. Elmer at Manhattan, Kansas, and Miss McCulloch at Washington. Machacek presented a paper at the meeting of the Quebec Society for the Protection of Plants, at MacDonald College, March 30, 1927; after this he mailed his culture to Thom for identification without information as to his announcement of it as new. The culture was received May 4, 1927 and he was advised of its isolation and description in this country by McCulloch and Thom. He subsequently acknowledged that his paper had been presented at a meeting and gave the date of the presentation, but withheld the name and description used. The report containing his paper was received by the U. S. Department of Agriculture Library, April 3, 1928. In the intervening period both of Miss McCulloch's papers were published. There is no question as to the identity of the organisms reported. Thom (1930), therefore, substituted McCulloch and Thom's description of the species but ascribed priority of publication to Machacek.

The same usage is followed in this Manual, although Wakefield and Moore (1936), after reviewing the history of the species, concluded that it should be cited as *Penicillium gladioli* McCulloch and Thom.

The conidial form described and figured by McCulloch and Thom was reported to comply closely with the description of *Penicillium divergens* Bainier and Sartory (1912), and might have been identified with it except for the entire lack of sclerotia in that species.

Occurrence and Significance

Penicillium gladioli is commonly found on gladiolus corms, and under some storage conditions may be responsible for substantial losses due to rot. It is occasionally isolated from soil. The species appears to be latently pathogenic to other plants producing fleshy root stocks or bulbs.

For controlling the Penicillium-rot of gladiolus corms, Machacek (1927) recommended the following measures: care in digging, dry storage, dusting with copper carbonate or copper sulfate, periodic removal of diseased corms, and judicious selection of corms for planting. McCulloch and Thom (1928) reported the use of mercuric chloride and commercial fungicides as means of control. White (1934) obtained good results with a mercury ammonium silicate dip. Dodge and Laskaris (1941) found *P. gladioli* commonly associated with the *Botrytis* core-rot in gladiolus; recommended control measures included stringent field and storehouse sanitation, care in digging, and careful drying of all corms, especially those harvested in wet weather.

Limber (1944) isolated *Penicillium gladioli* from a diseased yam (*Dioscorea* sp.) from Cuba.

In one of their surveys of different fungi for the production of antibiotics, Wilkins and Harris (1943) reported *Penicillium gladioli* to produce an antibacterial substance that inhibited *Bacterium coli*, *Staphylococcus aureus*, and *Pseudomonas pyocyanea*. Subsequently Brian, *et al.* (1946a) re-examined the species and found that a substance possessing both antifungal and antibacterial properties was produced. The antibiotic was designated "gladiolic acid". Methods for producing and concentrating the active substance were briefly noted, as were also its chemical properties. The substance prevented the germination of *Botrytis allii* conidia at a concentration of 2μg./ml.

Penicillium ochraceum Series

Outstanding Characters

Colonies with conidial areas variously in yellowish olive, buffy olive, or buffy brown in some strains, in others showing lighter shades near sandy brown or pinkish buff, but never developing gray-green, blue-green, or yellow-green shades.

Conidiophores mostly arising independently from the substratum or from a well developed aerial felt to produce a deep velvety effect, variable in length up to 400 to 500μ, with walls roughened; not infrequently aggregated into definite fascicles, particularly in older cultures on malt agar.

Penicilli variable in size but usually showing one or more branches in addition to the main axis, terminating in metulae and sterigmata and bearing tangled chains of conidia.

Colonies upon most media produce an earthy or moldy odor, often very strong.

Series Key

1. Colonies lacking true green colors in areas of ripe conidia *P. ochraceum* series
   a. Conidial areas in yellowish olive, buffy olive or buffy brown shades.
      P. ochraceum (Bainier) Thom
   b. Conidial areas in lighter shades near sandy brown or pinkish buff.
      P. carneo-lutescens Smith
   c. Conidial areas colorless or in light cream shades.
      Color mutants of *P. urticae* and other species

Two well marked species comprise this easily recognizable series, namely: *Penicillium ochraceum* (Bainier) Thom and *P. carneo-lutescens* Smith. The former, as the name implies, is characterized by conidia that superficially appear predominantly yellow-brown, although an olive coloration is usually detectable when conidial areas are compared with reference color charts. The latter species shows a lighter coloration, usually in sandy to pinkish buff shades. The degree of relationship between the species is not known, and they are considered together largely as a matter of convenience.

Penicillium ochraceum commonly produces heavily sporulating colonies which superficially appear deeply velvety or lanose. Largely in recognition of this latter aspect Thom (1930) placed the species in his section Lanata. Thorough comparative study of this species in relation to other members of the Asymmetrica that produce branched penicilli now convinces us that it more properly belongs in the Fasciculata. Although *P. ochraceum* is representative of a series based primarily upon the non-green color of its conidia, attention should be called to the tendency for this species to blend into the *P. viridicatum* series, next to be considered. This probable relationship should not be overlooked, should any physiological or biochemical study of either series assume importance.

Penicillium carneo-lutescens Smith is allied to *P. ochraceum* primarily upon the basis of spore color. Colonies are usually deeper and show a more consistent and marked fasciculation. The species is regarded as possibly based upon a non-green natural mutation of some cosmopolitan species such as *P. expansum* Link or *P. corymbiferum* Westling. Lacking proof of such origin, the species is retained; nevertheless, natural mutations with white to light tan or even pinkish conidia have been encountered frequently enough to establish this possibility.

Penicillium ochraceum (Bainier) Thom, in The Penicillia, pp. 309–310. 1930.

Colonies on Czapek's solution agar attaining a diameter of 3.0 to 3.5 cm. in ten days at room temperature, in some strains more or less floccose, 2 to 3 mm. deep, in others almost velvety, azonate at first but commonly becoming definitely zonate in age, radiately furrowed, bearing abundant conidial structures particularly along inter-colony margins (fig. 123A), growing margins white to dull buff in color, conidial areas becoming yellowish olive to dark greenish olive or buffy olive (Ridgway, Pl. XXX) when mature; exudate generally abundant, colorless; odor very pronounced, penetrating, earthy; reverse in dull yellow to vinaceous shades; conidiophores abundant, arising from submerged hyphae or from a well developed aerial felt, 100 to 200μ or more in length by about 4.0μ in diameter, with walls conspicuously roughened; penicilli asymmetric, approximately 20 to 35μ in length, usually showing one or more branches terminating in verticils of metulae and sterigmata (fig. 123C), sometimes showing metulae and sterigmata only, branches and metulae finely roughened, metulae and sterigmata more or less divergent and conidial chains either tangled or tending to adhere into loose columns 50 to 100μ in length; branches 15 to 25μ long by 3.0 to 3.5μ; metulae about 10 to 12μ by 2.5 to 3.0μ; sterigmata 8 to 10μ by 2.0 to 2.5μ; conidia globose to subglobose, commonly 3.0 to 3.5μ but ranging from 2.5 to 4.0μ, with larger cells occasionally observed, walls delicately roughened, appearing slightly yellowish in mass under the microscope.

Colonies on steep agar 3.0 to 4.0 or 4.5 cm. in ten days at room temperature, generally deeper than on Czapek, ranging from floccose to clearly fasciculate (fig. 123B), sporulating more abundantly but with color and general colony pattern as above, conidiophores and penicilli as described on Czapek.

Colonies on malt agar growing more rapidly, spreading, attaining a diameter of 5 cm. in ten days, generally plane except slightly raised in central area, loose-textured with tendency to become floccose, more or less zonate in marginal areas, commonly becoming definitely fasciculate in age, sporulating abundantly, with coloration in lighter shades than on Czapek or steep agars; conidial structures essentially as above, but with conidiophores more conspicuously roughened and elements of the penicillus slightly heavier.

The name is based upon an unpublished usage by Bainier. Among the cultures received by Thom in 1922 from the Bainier Collection through Dr. daFonseca was a tube labeled "*P. ochraceum*". Adopting the name, Thom (1930) made this the basis of a new species based primarily upon the dis-

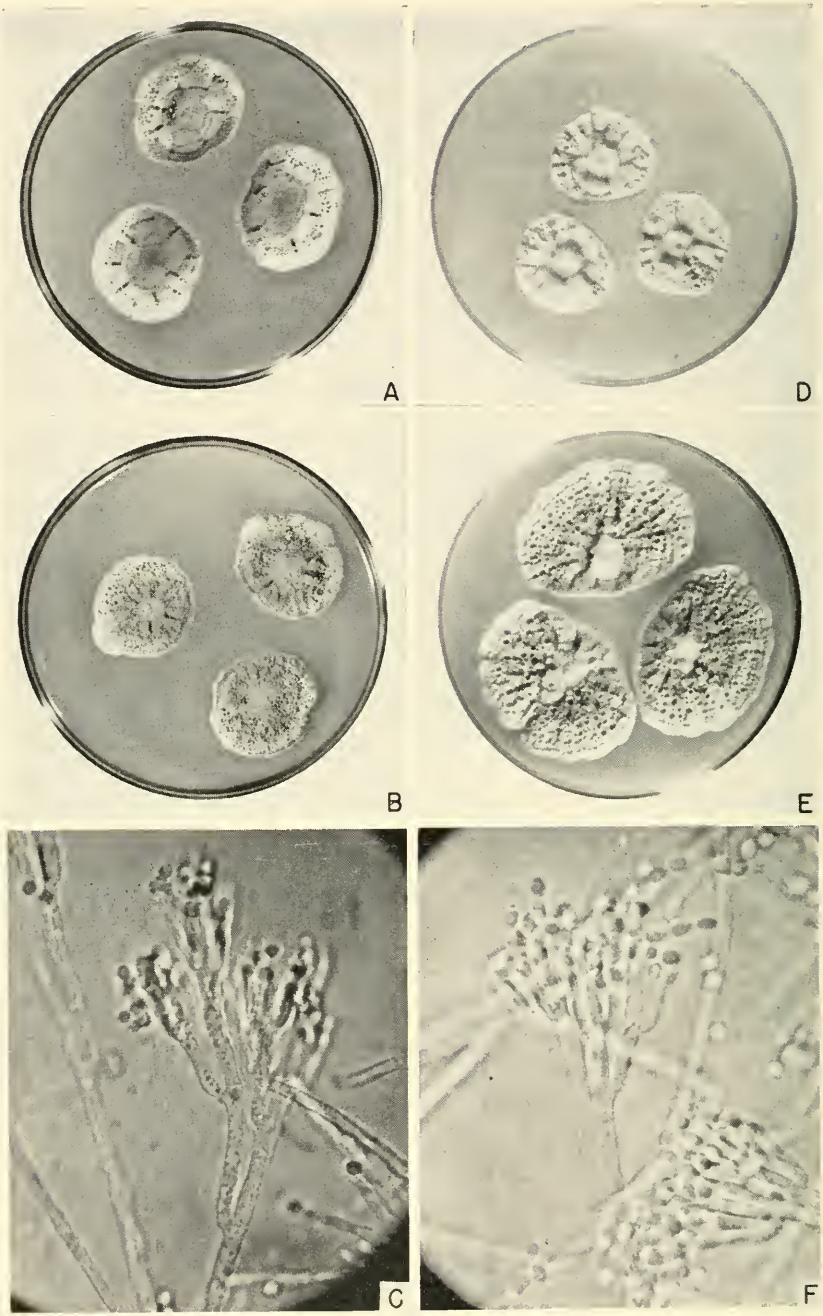


FIG. 123. *Penicillium ochraceum* series. *A* and *B*, *P. ochraceum* (Bainier) Thom, NRRL 869, on Czapek and steep agars at 10 days. *C*, Detail of penicillus showing characteristically roughened conidiophore, × 750. *D* and *E*, *P. carneo-lutescens* Smith, NRRL 2035, on Czapek and steep agars at 10 days. *F*, Detail of penicillus, × 750.

tinctive coloration of its conidial heads. The species is occasionally encountered in the routine examination of molds from soil or organic materials undergoing slow decay.

Represented in the present study by strain NRRL 871 from the Biourge collection, and strains NRRL 869 and 870 which represent sub-cultures derived from Thom's No. 4424 (cited in 1930).

Members of this series show a tendency to vary markedly in culture, with sector variants commonly appearing in cultures long maintained in the laboratory. Strains NRRL 869 and 870 are of this origin and differ in the following particulars. NRRL 869: colonies deeply floccose, 2 to 3 mm. deep, buffy brown in color, and showing little or no trace of the olive color often associated with this species. NRRL 870: colonies rather close-textured, strongly wrinkled and folded, heavily sporulating, comparatively thin, 200 to 300μ deep, and colored in dark greenish olive shades. The latter strain is strongly suggestive of certain members of the *Penicillium viridicatum* series. Penicilli and supporting conidiophores in the two substrains are essentially alike.

Thom (1930) originally assigned *Penicillium ochraceum* to his section Lanata, emphasizing the lanose colony character which seemed predominant. More detailed examination of this species in our present study shows strains to be very variable, and to almost always develop some fasciculation in older colonies, especially upon malt extract agar. This character, in particular, dictates the present assignment.

Penicillium ochraceum var. *macrosporum* Thom, in The Penicillia, p. 310. 1930. Examining the members of this series Thom observed that certain strains produced conidia averaging somewhat larger than the type strain as received from the Bainier collection. This difference in spore size seemed to be consistent enough to warrant the description of a new variety, *macrosporum*. Re-examination of strains then in his possession and the study of some new material has led us to reconsider the validity of this designation. Strain NRRL 873, from the Thom collection as $4742P_3$ and one of the original types, does produce conidia consistently larger than listed for the species, averaging about 4.0 to 4.5μ instead of 3.0 to 3.5μ. However, limited numbers of large conidia are generally observed in the typically smaller-spored forms. Furthermore, the measurements and pattern of the penicilli in the large- and small-spored forms are the same. We, therefore, believe that the large-spored form probably represents a variant from this species which is not sufficiently marked to warrant continued varietal recognition.

Penicillium carneo-lutescens Smith, in Brit. Mycol. Soc. Trans. **22** (3/4): 253–254; Pl. XVI, fig. 6. 1939.

Colonies on Czapek's solution agar growing somewhat restrictedly, attaining a diameter of 3.0 to 3.5 cm. in 2 weeks at room temperature, comparatively deep up to 2 to 3 mm. in central areas, more or less floccose, with surface irregular, commonly tufted and furrowed (fig. 123D), heavily

sporing in marginal and submarginal areas, usually granular from fasciculate arrangement of conidiophores, less commonly almost velvety with growing margin irregular, usually 1.0 to 1.5 mm. wide, white but quickly becoming colored (see above) in pale sandy brown shades approximating pinkish buff (Ridgway, Pl. XXIX) with the ripening of conidia; exudate usually limited, clear; odor moldy, not strong; reverse in orange-red shades, ranging from vinaceous pink to cacao brown (R., Pl. XXVIII); penicilli comparatively large, mostly 35 to 50μ in length, but ranging from 25 to 60μ and bearing tangled conidial chains up to 50μ or more in length, borne upon conidiophores up to 500μ by 3.5 to 4.0μ with walls finely roughened; penicilli asymmetric, irregular in pattern, usually consisting of one or two more or less appressed branches in addition to the main axis (fig. 123F); branches mostly 15 to 20μ by 2.8 to 3.3μ, occasionally larger or smaller, with walls finely roughened; metulae usually in clusters of 3 to 5, mostly 10 to 12μ by 2.5 to 3.3μ, but ranging from 9 to 15μ in length; sterigmata numbering about 5 in the verticil, 8 to 10μ by 2.5 to 2.8μ; conidia elliptical when first formed, commonly becoming subglobose in age, 3.0 to 3.5μ, with walls smooth or very faintly roughened.

Colonies on steep agar more rapidly growing than on Czapek, 5.0 to 5.5 cm. in 2 weeks (fig. 123E), but otherwise essentially as described above; exudate abundantly produced, clear, collecting into conspicuous drops along radial lines; odor pronounced, somewhat moldy; penicilli generally as above but smaller and frequently appearing fragmented or underdeveloped.

Colonies on malt agar growing rapidly, 5.0 to 6.0 cm. in 2 weeks, loose-textured, floccose, about 2 mm. deep, very light sporing, white to very pale buff, showing a definite tendency to develop fasciculate hyphal bundles (mostly sterile) at the margins; penicilli as on Czapek except very conspicuously roughened even to the sterigmata, with central portions of metulae and sterigmata commonly inflated.

The type strain was isolated in 1939 from dried Kentish hops by George Smith, London School of Hygiene and Tropical Medicine, and in the same year was deposited in the Centraalbureau at Baarn. The above diagnosis is based upon Smith's original description together with our own observations on his culture which was sent to us in February 1946 by the Centraalbureau. The culture is maintained in our Collection as NRRL 2035. Insofar as we know, no additional isolations have been made.

The exact relationships of this species remain in doubt. Possibly it represents a color mutation from some species such as *Penicillium corymbiferum* Westling. Irrespective of its true relationship, we believe that it can be assigned to the series with *P. ochraceum* more satisfactorily than elsewhere and separated upon the basis of conidial pigmentation.

Occurrence and Significance

Members of the present series appear to be comparatively rare in nature. *Penicillium ochraceum* has been infrequently isolated from grain, decaying vegetation, and soil. *Penicillium carneo-lutescens* is known only from the type source, dried Kentish hops. Whereas proof of such origin is lacking, both species may possibly represent color mutations from other more common species.

No biochemical or physiological study of either species is known to us.

Penicillium viridicatum Series

Outstanding Characters

Colonies are typically bright yellow-green to dark yellow-green in color, commonly approximating "prasinus" or "viridis" of Saccardo's Chromotaxia, hence the name. Bluish shades are generally transient or lacking altogether. Colonies often become light brown in age, or in other strains may remain persistently green upon most media.

Conidiophores may be sufficiently aggregated into clusters, or fascicles, to give the colony surface a definitely tufted appearance; or they may occur as a mixed stand of simple and clustered conidiophores to produce a granular effect; or in other strains they may be mostly single to produce an essentially velvety effect with little or no outward evidence of a fasciculate relationship; they are usually rough-walled.

Penicilli are comparatively large and usually consist of one or two branches in addition to the main axis, with each major element bearing successively verticils of metulae and sterigmata.

All produce a strong, penetrating, moldy or earthy odor.

Series Key

a. Colonies typically in bright yellow-green to dark yellow-green shades; conidiophores usually rough-walled ..... *P. viridicatum* series

1′. Conidial areas showing bright yellow-green shades, at least when young.

aa. Colonies remaining bright yellow-green in age or tardily becoming light brown; odor pronounced ..... *P. viridicatum* Westling

bb. Colonies at first bright yellow-green but quickly becoming dull and often showing vinaceous shades in older areas; odor very strong. *P. olivino-viride* Biourge

2′. Conidial areas quickly developing dark yellow-green shades. *P. palitans* Westling

Members of this series are less common than members of the *Penicillium cyclopium* and *P. expansum* series, yet are not infrequently encountered among cultures submitted for diagnosis, or among strains newly isolated from natural substrata. They occur frequently upon decaying vegetation in contact with the soil. Occasional strains assignable here cause a

limited rot when inoculated into pomaceous fruits, and members of the series are occasionally isolated from natural infections of this kind. Rather close relationship to the *P. expansum* series appears indicated, since strains apparently intermediate between the two series are sometimes encountered. They are not, however, encountered as a cause of economic losses in apples and related fruits.

Definite color differences usually serve to differentiate between the *Penicillium viridicatum* series and *P. ochraceum* (Bainier) Thom. However, colonies of the latter (consistently in certain strains and in occasional sector variants of almost any strain) may show dull, olive-green to brown colors definitely suggestive of some members of the *P. viridicatum* series.

A number of species apparently assignable to the *Penicillium viridicatum* series have been described (Thom, 1930), and individual strains can be found which seem to duplicate most of them with reasonable exactitude. Such differences as occur, however, are often found to assume minor significance when large numbers of isolates are observed. Characters which may appear clearly diagnostic when four or five strains are examined are found to intergrade and show progressive change when the comparison is extended to many cultures. Of the several species that have been described, we believe that three can be recognized within the series, as indicated in the key above.

Of these species, *Penicillium viridicatum* Westling is the most widely distributed and the most representative. It is characterized principally by bright yellow-green colors usually associated with a marked fasciculation of conidiophores. Colonies of *P. psittacinum* Thom show a similar pigmentation, and this species may be more nearly related to *P. viridicatum* than is indicated by the placement given the two species in this Manual (see p. 448). *Penicillium psittacinum*, in its typical aspect, shows a funiculose arrangement of aerial hyphae but no definite upright bundles of conidiophores such as characterize the Fasciculata. *Penicillium olivinoviride* Biourge usually produces less fasciculate colonies, which on Czapek quickly develop dull olive to gray and on steep agar purplish or vinaceous shades. *Penicillium palitans* Westling, as understood by us, grows somewhat more rapidly than either of the preceding species and quickly develops dark rather than bright yellow-green shades which are usually persistent in age. This last species is regarded as somewhat transitional in the direction of the *P. expansum* series.

Penicillium viridicatum Westling, in Arkiv för Botanik **11:** 53, 88–90, figs. 14 and 56. 1911. Thom, The Penicillia, p. 394. 1930.

Colonies on Czapek's solution agar (Col. Pl. VIII) generally restricted, usually attaining a diameter of 2.5 to 3.5 cm. in 12 to 14 days at room

PLATE VIII

TOP: Penicillium viridicatum Westling, NRRL 963, on Czapek's solution agar, 10 days. *CENTER: Penicillium martensii* Biourge, NRRL 2029, on Czapek's solution agar, 10 days. *BOTTOM: Penicillium corymbiferum* Westling, NRRL 2032, on Czapek's solution agar, 10 days. (Color photographs by Haines, Northern Regional Research Laboratory. Reproduced through co-operation of Chas. Pfizer & Co., Inc.)

temperature, often more or less zonate, in some strains strongly fasciculate, in others loose-textured approaching floccose but showing a limited development of fascicles or tufts (fig. 125A), and in still others essentially velvety, or scantily "granular" in the marginal area, usually showing few to many radial furrows, heavily sporing throughout in some strains, less heavily sporing in others with conidial development heaviest in marginal to submarginal zones, conidial areas when young characteristically in bright yellow-green shades near fluorite green to deep malachite green (Ridgway, Pl. XXXII) in some strains to greenish glaucous or pistachio green (R., Pl. XLI) in others, darkening in age but usually remaining persistently green; exudate abundantly produced in some strains, not in others, clear to pale yellow; odor strong, moldy, and in some strains sourish; reverse at first colorless to yellowish, in some strains remaining so, in others becoming dull brown in age. Penicilli comparatively large, up to 65 to 70μ in length, bearing conidia usually in tangled chains up to 100 to 150μ long or in irregular and poorly defined columns (fig. 124A); conidiophores commonly 150 to 250μ by 3.5 to 4.5μ but variable and occasionally longer up to 400μ in length and 6.0 to 6.5μ in diameter, with walls typically roughened; penicilli often irregular, with branches, metulae and sterigmata not consistently produced at different levels, usually showing 1 to 3 branches 20 to 40μ by 3.5 to 4.0μ, in addition to the main axis (fig. 124B), occasionally showing secondary branches, with each branch or sub-branch bearing 4 to 6 metulae, mostly about 12 to 16μ by 3.0 to 4.0μ but occasionally larger or smaller; sterigmata commonly in clusters of 5 to 8 and measuring 7 to 10μ by 2.2 to 3.0μ, usually borne at approximately the same level in some strains, not in others; conidia elliptical when first formed, often remaining so and measuring up to 4.5 by 3.3μ, mostly becoming subglobose, 3.0 to 3.5μ in diameter, or occasionally up to 4.0 to 4.5μ, with walls delicately roughened (fig. 124C).

Colonies on steep agar growing somewhat more rapidly than on Czapek, but retaining the same general pattern, heavier sporing in most strains, bright yellow-green in young conidial areas and commonly remaining green in age; odor strong as on Czapek; conidiophores less consistently roughened; penicilli as described above; conidia more consistently elliptical and commonly less roughened than above.

Colonies on malt agar varying markedly, in some strains spreading, plane, heavily sporing, and somewhat granular (fig. 125B); in others restricted, velvety or tufted in the marginal area only; odor pronounced, in some strains suggesting fresh mushrooms; penicilli generally shorter and less variable in length, tending to be compact; conidiophores conspicuously roughened; conidia, for the most part, smooth-walled and commonly remaining elliptical, often measuring 4.5μ by 3.0μ.

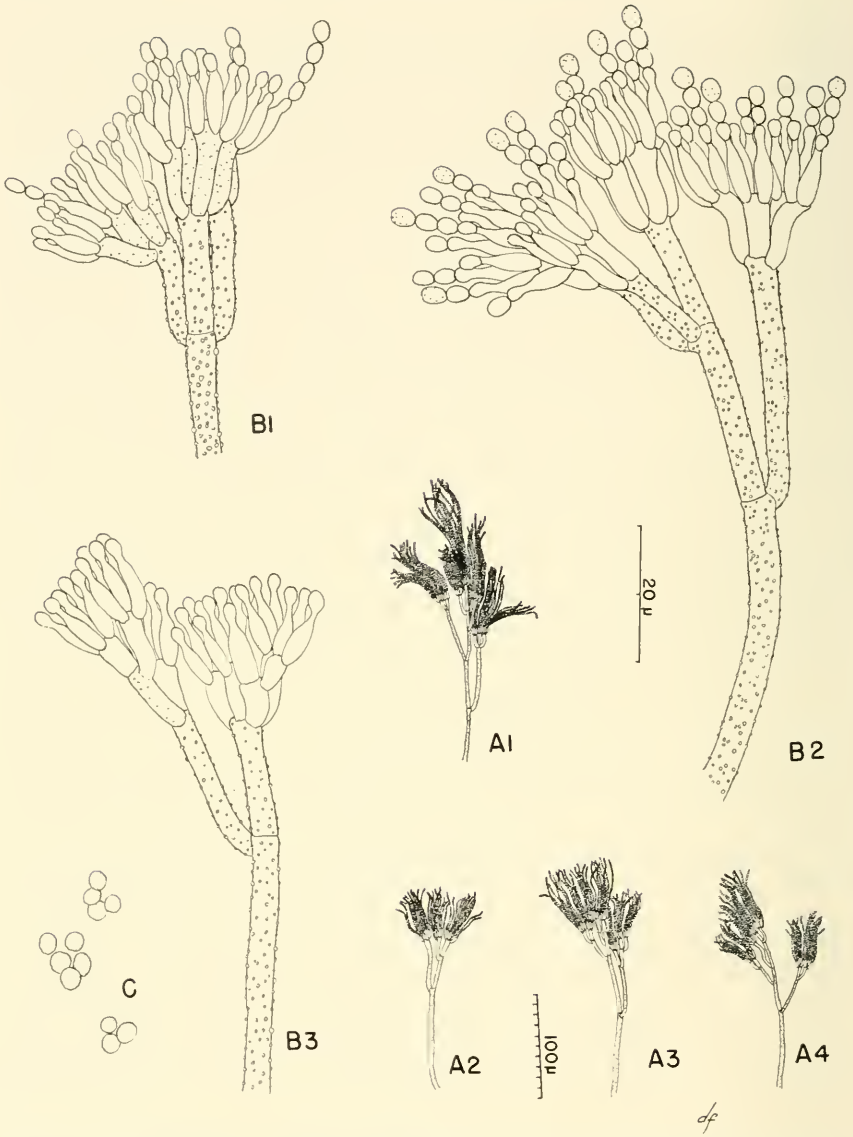


FIG. 124. *Penicillium viridicatum* Westling. A_1–A_4, Habit sketches of typical penicilli. B_1–B_3, Camera lucida drawings showing details of cellular structure and common variations in pattern among representative penicilli. *C*, Mature conidia.

Species description based upon NRRL 963 isolated as an air contaminant in 1940, in Washington, D. C. This culture normally produces colonies that are strongly fasciculate. The species is also represented by

FIG. 125. *Penicillium viridicatum* series. *A* and *B*, *P. viridicatum* Westling, NRRL 963, on Czapek and malt agar at 10 days. *C* and *D*, *P. olivino-viride* Biourge, NRRL 2028, as the preceding. *E* and *F*, *P. palitans* Westling, NRRL 966, as above.

NRRL 1160 and 1161 isolated from agar plates exposed in a meat-packing plant and sent to us in 1937 by Dr. G. A. Ledingham, Ottawa, Canada. Strain NRRL 965 received from the Thom Collection (No. 4733.125) as Biourge's culture of *Penicillium verrucosum* Dierckx is believed to be properly assigned here. NRRL 958 received in 1927 from Professor F. D. Heald, Pullman, Washington, is also representative of this species in the broad sense of this Manual. This latter strain produces colonies that are conspicuously zonate and approach the "*blue*-green series," as typified by *P. cyclopium*, but remain conspicuously green in age.

Penicillium musae Weidemann (Centbl. f. Bakt. etc., (II) **19:** 687–689, fig. 3. 1907), isolated from yellow-brown to olive-brown patches on a banana, was described in terms which indicate its relationships with *P. viridicatum* Westling, particularly in the yellow-green color of its conidia and in the branching habit of the penicillus described. Vegetative hyphae were reported as 2.5μ in diameter, which is considerably less than in most members of the series. Conidia were described as elliptical to subglobose and to measure about 2.2 to 2.8 by 2.0 to 2.3μ, or to be appreciably smaller than in the strains examined by us. Although the strain originally observed obviously represented a comparatively delicate form, we believe the species probably should be regarded as a synonym of the generally accepted species *P. viridicatum* Westling.

Penicillium stephaniae Zaleski (Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 451–452; Taf. 40. 1927) was based upon a strain isolated from soil in Poland. The type was received from the Centraalbureau in 1928 and studied by Thom, who, in his Monograph (1930), confirmed Zaleski's general observations regarding it. Both the original description and Thom's notes, subsequently made, point to inclusion in the *P. viridicatum* series. In the absence of the type or other authentic material for comparison in the present study, specific assignment to *P. viridicatum* Westling or *P. olivino-viride* Biourge is not recommended, but we question whether adequate bases exist for retention of *P. stephaniae* as a separate species.

Penicillium verrucosum Dierckx (Soc. Scien. Brux. **25:** 88. 1901. See also Biourge, Monograph, La Cellule **33:** 123–126, Col. Pl. I, Pl. II, fig. 7. 1923) has been commonly interpreted as representing a member of the *P. viridicatum* series which shows conidial structures with conidiophores and branches conspicuously roughened. Since this character varies markedly in different members of the series, and since it differs greatly in the same strain depending upon the substratum employed, a species based primarily upon this character is of questionable validity. Culture NRRL 965, from the Thom Collection as No. 4733.125 representing Biourge's culture of *P. verrucosum* differs little from other strains regarded by us as *P. viridicatum*, whereas a strain received from the Centraalbureau in May 1946, and presumably identical as to source, should more properly be assigned to the *P. cyclopium* series. The name *P. verrucosum* should, we believe, be dropped.

Penicillium blakeslcei Zaleski (Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 441–444, Taf. 36. 1927) as received and studied by Thom (1930) represented a mixture of two molds, one white or nearly so, the other green and conforming fairly closely to Westling's *P. viridicatum*. Assuming that the latter culture represented Zaleski's species, *P. blakesleei* may be regarded as belonging to the series under dis-

cussion and probably differing from *P. viridicatum* only within the range of interspecies variation. No cultures under the name were available for the present study.

Penicillium olivino-viride Biourge, in Monograph, La Cellule **33:** fasc. 1, pp. 132–133, Col. Pl. II and Pl. II, fig. 12. 1923. Thom, The Penicillia, pp. 393–394. 1930

Colonies on Czapek's solution agar growing rather restrictedly, attaining a diameter of 2.5 to 3.0 cm. in 10 to 12 days at room temperature, appearing almost velvety in some strains, loose-textured to almost floccose in others, usually marked by a limited number of comparatively deep and conspicuous radial furrows (fig. 125C), heavily sporing throughout or with conidial development concentrated in marginal areas, with surface usually appearing more or less granular, with conidiophores usually arising singly from the substratum, but with fascicles or bundles often produced near the colony margin and less commonly in more central areas, with growing margin about 1 mm. wide, white, shading quickly to the yellow-green shades characteristic of the series, approximating asphodel or pois green (Ridgway, Pl. XLI), then changing to sage green to slate olive (R., Pl. XLVII), and finally in age becoming mouse gray (R., Pl. LI) to light brown shades; exudate limited in amount, usually clear; odor very strong, penetrating, "earthy"; reverse at first colorless or light yellowish, becoming light brown to smoky or slightly purplish in age; penicilli comparatively large with conidia borne in tangled chains up to 50 to 100μ (rarely 150μ); conidiophores 3.3 to 4.0μ in diameter and up to 250μ in length, with walls smooth or definitely roughened; penicilli usually showing one or two branches in addition to the main axis, generally more or less appressed, ranging from 15 to 30μ by 3.0 to 3.5μ; metulae borne in clusters of 3 to 5 on each branch and the main axis, usually 8 to 12μ by 2.5 to 3.5μ, with occasional sterigmata arising from the same node; sterigmata mostly 8 to 10μ by 2.2 to 2.8μ usually in verticils of 3 to 6, in some penicilli borne at approximately the same levels, in others at different levels; conidia globose to subglobose, mostly 3.3 to 4.0μ in diameter, with walls delicately roughened.

Colonies on steep agar essentially as described above but in most strains more conspicuously and more closely furrowed, generally heavier sporing but with conidial areas soon developing a purplish-vinaceous color approximating vinaceous gray shades (R., Pl. L) to drab shades (R., Pl. LI); fasciculation commonly lacking; odor pronounced as on Czapek; penicilli generally larger and more complexly branched but of the general pattern described above; conidiophores less commonly roughened; occasional conidia appearing elliptical.

Colonies on malt agar plane, spreading, often but not consistently heavy sporing, with color tending to remain yellow-green in age, more or less

zonate (fig. 125D); penicilli definitely shorter and more compact than upon the above media, with conidiophores consistently and conspicuously roughened.

Species description based upon NRRL 2028 received from the Centraalbureau in May 1946, as Biourge's strain representing this species. Duplicated essentially by NRRL 959 received by Thom from Biourge as his type in 1924. This culture now produces colonies somewhat more loose-textured than that received from Baarn but is otherwise similar to it. Strain NRRL 961, received from Carrera in Buenos Aires in 1940, is considered to be entirely representative of the species as considered here. Strain NRRL 962 (Thom's No. 3028) differs from the above in producing colonies with young conidial areas in brighter yellow-green shades near fluorite green (R., Pl. XXXII), but with older conidial areas showing the purplish vinaceous colors that characterize the species. Thom (1930) considered the last mentioned strain as representative of the *Penicillium viridicatum* series only, but the close similarity of this form to the type material cited above leads us to the present more specific assignment.

Penicillium palitans Westling, in Arkiv för Botanik **11:** 53, 83–86, figs. 12 and 54. 1911. Thom, The Penicillia, pp. 396–397. 1930.

Colonies on Czapek's solution agar attaining a diameter of 3.5 to 4.0 cm. in 12 to 14 days at room temperature, ranging from about 300 to 500μ deep in marginal to submarginal areas up to 1 to 2 mm. in colony center, surface appearing granular or mealy but generally not conspicuously fasciculate, often narrowly zonate (fig. 125E) with shallow to prominent radial furrows, growing margin white, about 1 mm. wide, heavily sporing throughout in most strains, at first in greenish glaucous shades through pistachio green to shades of American green (Ridgway, Pl. XLI) or Russian green (R., Pl. XLII) at maturity, becoming grayish olive in age (R., Pl. XLVI); often tending to develop limited areas of white sterile overgrowth; exudate clear or light amber, abundantly produced in some strains, not in others; odor pronounced, moldy; reverse colorless at first, through dull yellow shades to pale brown and finally light purplish brown; penicilli asymmetric, comparatively large, mostly 40 to 50μ in length but ranging from 30 to 70μ and bearing tangled, divergent, or loosely parallel conidial chains up to 100μ or more in length; conidiophores mostly 100 to 200μ by 3.5 to 4.0μ in some strains, definitely longer in others up to 300 to 400μ, with walls roughened; penicilli generally showing 1 or 2 branches in addition to the main axis, branches typically appressed and often unequal in the same penicillus, commonly ranging from 15 to 25μ or more by 3.0 to 3.5μ; bearing metulae in groups of 3 to 5, mostly 10 to 15μ by 2.8 to 3.3μ; sterigmata usually borne in compact verticils of 5 to 7, measuring 8 to 10μ by 2.2 to 3.0μ; conidia elliptical when first formed, then globose to subglobose,

mostly 3.5 to 4.0μ in diameter but ranging up to 4.5 or even 5.0μ, with walls comparatively heavy, smooth or nearly so.

Colonies on steep agar growing more rapidly, attaining a diameter of 5.0 to 5.5 cm. in 12 to 14 days, but essentially duplicating the above in pattern, texture, and color; penicilli as described above.

Colonies on malt agar 4.0 to 5.0 cm. in 12 to 14 days, comparatively thin, heavily sporing, plane (fig. 125F), except for a slight flocculent overgrowth in colony centers, marginal areas appearing granular, approximately sage green (R., Pl. XLVII) to Russian green (R., Pl. XLII) with reverse in dull peach shades; penicilli as on Czapek agar but generally showing less irregularity in branching.

Species description centered upon NRRL 966 isolated in the summer of 1940 as a laboratory contaminant in Washington, D. C., and diagnosed as *Penicillium palitans*. The species is also represented by NRRL 2033 received in May 1946, from the Centraalbureau as a strain of *P. palitans* originally from Westling; NRRL 1164, from G. A. Ledingham, Ottawa, Canada, in 1940, as an isolate from pulp-mill waste; and three cultures under this name received in July 1947 from George Smith, London School of Hygiene and Tropical Medicine as strains studied by Birkinshaw and Raistrick (1936). NRRL 914, an isolate from pears, received in 1939 from Professor Heald, Pullman, Washington, approximates the species.

The strain received from the Centraalbureau as *Penicillium palitans* of Westling probably represents the type culture. It is, however, somewhat looser in texture than most strains believed by us to represent this species. Our description above is written in broad enough terms to include Westling's strain, together with thinner- and closer-textured strains such as NRRL 966 and 1164. The penicilli in all of these cultures are identical.

Penicillium palitans is believed to be closely related to *P. viridicatum*, hence is included in the series with it. It differs from the latter species, however, in producing colonies which are typically darker yellow-green, often less fasciculate, and show conidia usually larger. Certain strains believed to represent the species show characteristics which suggest *P. cyclopium* Westling.

While *Penicillium palitans* is assigned in the *P. viridicatum* series, largely upon the color of conidial areas and the character of its conidial structures, many strains fail to show definite fasciculation. The colony surface of all strains, however, may be regarded as "mealy". Placement here seems to be more logical than elsewhere.

Occurrence and Significance

Penicillium viridicatum and allied species commonly occur in soil. From their distribution and number, they are assumed to play an active role in the slow aerobic decomposition of organic residues.

Members of the series appear to be abundant upon stored grain, particularly corn. Koehler (1938) reported *Penicillium viridicatum* and *P. palitans* capable of growing upon shelled corn at moisture levels of 17.6 per cent and 18.0 per cent, respectively. The latter species produced typical "blue-eye" damage, *i.e.*, developed abundant fruiting structures between the germ and seed coat, at 19.5 per cent moisture. Semeniuk and Barre (1944), investigating corn stored in steel bins in Iowa, found *P. viridicatum* to be the chief mold present, although *Aspergillus flavus* and *A. glaucus* were also reported. Marchionatto (1942a), working in Buenos Aires, found a *Penicillium*, identified by Thom as *P. viridicatum*, prevalent upon maize infected with "mildew". Such grain was reported to the Argentina Ministry of Agriculture as the cause of poisoning of pigs and horses. In a second report (1942b) both *P. viridicatum* and *P. olivino-viride* were noted as common on "moldy" maize, whereas *A. flavus* was most abundant.

Penicillium viridicatum and *P. palitans* are sometimes isolated from rotting pomaceous fruits, although they do not cause a destructive rot comparable to that produced by *P. expansum* (see p. 518).

Members of the series likewise occur upon fat and protein rich substrata. Stokoe (1928), investigating the rancidity of coconut oil caused by *Penicillium palitans* found this to be largely due to the presence of various methyl ketones. Ledingham (personal correspondence) isolated members of the present series from plates exposed in a meat packing plant. Three of the four strains of *P. palitans* studied by Birkinshaw and Raistrick (1936) were isolated by Neill from discolored New Zealand cheddar cheese.

Birkinshaw and Raistrick (1936a) reported the production by strains of *Penicillium palitans* of a hitherto undescribed metabolic product, designated palitantin, $C_{14}H_{22}O_4$. Upon Raulin-Thom medium, the substance was produced by the type of the species, received from Baarn, and by Neill's three isolates (cited above), which had been received as *P. puberulum* Bainier. Maximum yields were obtained at low temperatures from 10° to 18°C. Palitantin was shown to be an unsaturated dihydroxyaldehyde. The preparation of various derivatives and oxidation and reduction products was described.

Penicillium cyclopium Series

Outstanding Characters

Colonies are characterized by conidial areas in blue-green (aeruginous) colors in which the blue element predominates, or is at least clearly evident, and a sufficient proportion of the conidiophores are generally aggregated into fascicles to give the colony surface a granular or tufted appearance, at least in marginal areas. Colonies in reverse often show

orange-brown to maroon shades, and in some strains appear definitely purplish.

Conidiophores are commonly roughened when borne on Czapek's solution agar and are consistently roughened when p roduced on malt extract agar.

Penicilli are comparatively large, and each usually shows one or two branches that are commonly appressed and which, together with the main axis, bear verticils of metulae and sterigmata to produce a rather loose and often somewhat irregular conidial apparatus.

Strong odors, which may be described as moldy or earthy, are regularly produced upon most culture media.

Series Key

b. Colonies typically in blue-green (aeruginous) shades, with the blue element predominant or at least usually clearly evident; conidiophores smooth or rough-walled..... *P. cyclopium* series

1′. Colonies in dull blue-green shades mostly azonate or indistinctly zonate; conidiophores on Czapek agar generally roughened; conidia usually subglobose.

aa. Colonies with surface usually granular or tufted, and with definite fascicles appearing at least in the marginal areas.

1″. Conidia smooth or delicately roughened..... *P. cyclopium* Westling

2″. Conidia rough-walled and globose or nearly so. *P. cyclopium* West. var. *echinulatum* n. var.

bb. Colonies with fasciculation often reduced and with sporulating surfaces often appearing velvety or lanose..... *P. puberulum* Bainier

2′. Colonies usually in brighter blue-green shades; often narrowly zonate; conidiophores smooth or finely roughened on Czapek agar; conidia usually elliptical.

aa. Colonies fairly rapidly spreading, heavily sporing on malt agar. *P. martensii* Biourge

bb. Colonies more restricted, non-sporulating or lightly sporulating on malt agar..... *P. aurantio-virens* Biourge

Members of the series are very abundant in nature and may be isolated from a wide variety of natural substrata. In many respects they bear a close resemblance to the *Penicillium expansum* series (next to be considered), and separation from the latter is often difficult. They do not, however, rot pomaceous fruits, although they can often be isolated from such fruits, having entered as saprophytes or possibly as secondary parasites.

Separation into species within the series is difficult and often unsatisfactory. The number of characters available for diagnostic use is limited and these often appear to vary independently. For example, details of microscopy cannot be consistently correlated with a particular cultural aspect. This type of variation regularly occurs among different strains as freshly isolated. The same strains likewise tend to vary during periods of successive recultivation and the production of variant growth types

either as overgrowths or in the form of sectors is not uncommon. Such variants can usually be perpetuated in culture, and often continue to exhibit differences equal to those observed between new isolates.

Resulting in part from strain individuality and natural variability among these forms, and in part from an apparent lack of appreciation of the materials examined by others, many different species, obviously closely related, have been described by different investigators working in different localities and generally at different times. The type strains of some of these species have been preserved and were available for the present study. Certainly some of the described species cannot be regarded as valid, while the selection of those which should be so considered must of necessity be somewhat arbitrary. We have endeavored to select those species which through common usage have become best recognized.

Based upon the sum of our observations and a re-examination of original descriptions and figures, we believe the series can be best subdivided into species, or species aggregates, centering around *Penicillium cyclopium* Westling, *P. puberulum* Bainier, *P. martensii* Biourge, and *P. aurantio-virens* Biourge. Cultures are encountered which do not fit completely either of the species presented here, but it is believed that separation along the lines proposed will differentiate between the vast majority of strains. To recognize additional species or to make the descriptions more restrictive would, it is believed, place unwarranted emphasis upon variation between individual strains. On the other hand, to recognize only a single species, *P. cyclopium*, would necessitate the preparation of a description which would have to be inclusive almost to the point of being meaningless.

Penicillium cyclopium Westling is the most abundant and the most characteristic species in the series. Typically it is characterized by colonies showing limited to pronounced fasciculation of conidiophores, a dull blue-green coloration, and other features as indicated in the series characters above. Strains vary materially, and isolates are encountered which merge imperceptibly into the other member-species. The globose, rough conidia of *P. cyclopium* var. *echinulatum* are regarded as sufficiently distinctive to warrant the description of this new variety. *Penicillium puberulum* Bainier is hardly fasciculate but possesses so many characteristics (cultural, morphological, and physiological) in common with *P. cyclopium* that it is placed here irrespective of colony surface and texture. In its most typical aspect *P. martensii* Biourge differs in producing colonies of bluer color, less definitely roughened conidiophores, and elliptical conidia. *Penicillium aurantio-virens* is much like the preceding, but differs from it in producing colonies on malt agar characterized by abundant yellow mycelia and little or no spore production.

Penicillium cyclopium Westling, in Arkiv för Botanik **11:** 55–56, 90–92, figs. 15, 57. 1911. Thom, The Penicillia, pp. 384–385. 1930.

Colonies upon Czapek's solution agar usually growing rapidly, attaining a diameter of 4.5 to 5.0 cm. in 12 to 14 days at room temperature, usually

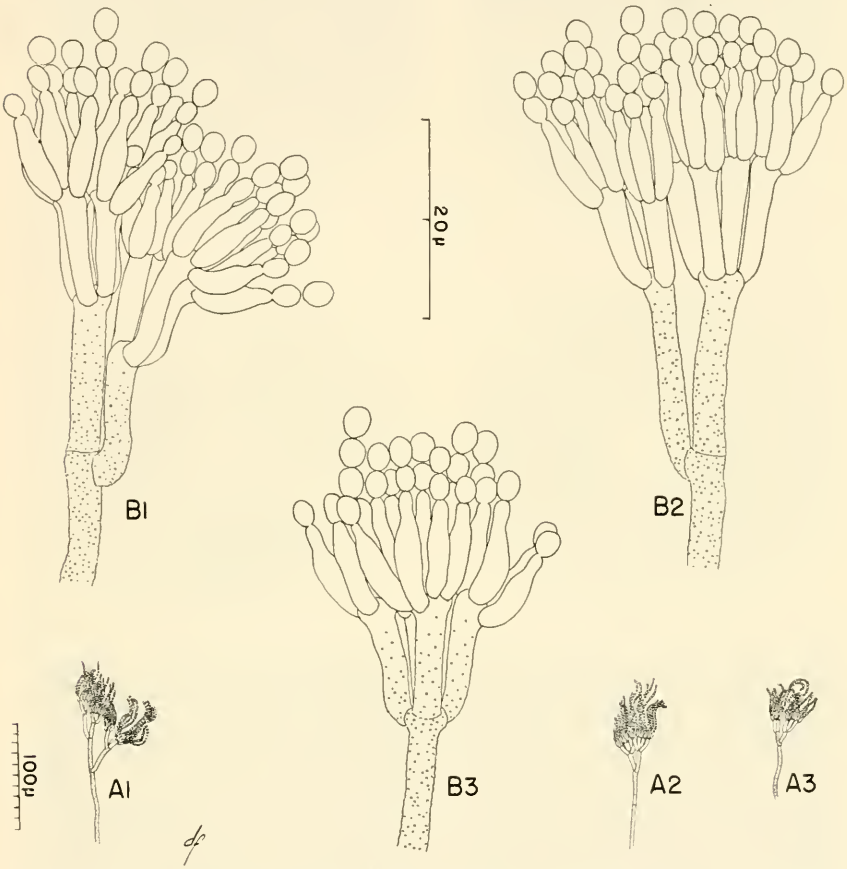


FIG. 126. *Penicillium cyclopium* Westling. A_1–A_3, Habit sketches of representative penicilli. B_1–B_3, Detailed drawings showing cellular structure of same; note roughened conidiophores and branches.

more or less radially furrowed, from 500μ to 1000μ deep, azonate or broadly zonate in age, in some cultures tending to develop limited sterile overgrowths, with margin compact, white, 1 to 2 mm. wide during the growing period (fig. 127A), often thinning in age, heavily sporing throughout and shading quickly through light bluish or green shades in young conidial areas to deeper shades near bluish gray-green (Ridgway, Pl. XLII), artemisia green or lily green (R., Pl. XLVII) at maturity, with surface typically ap-

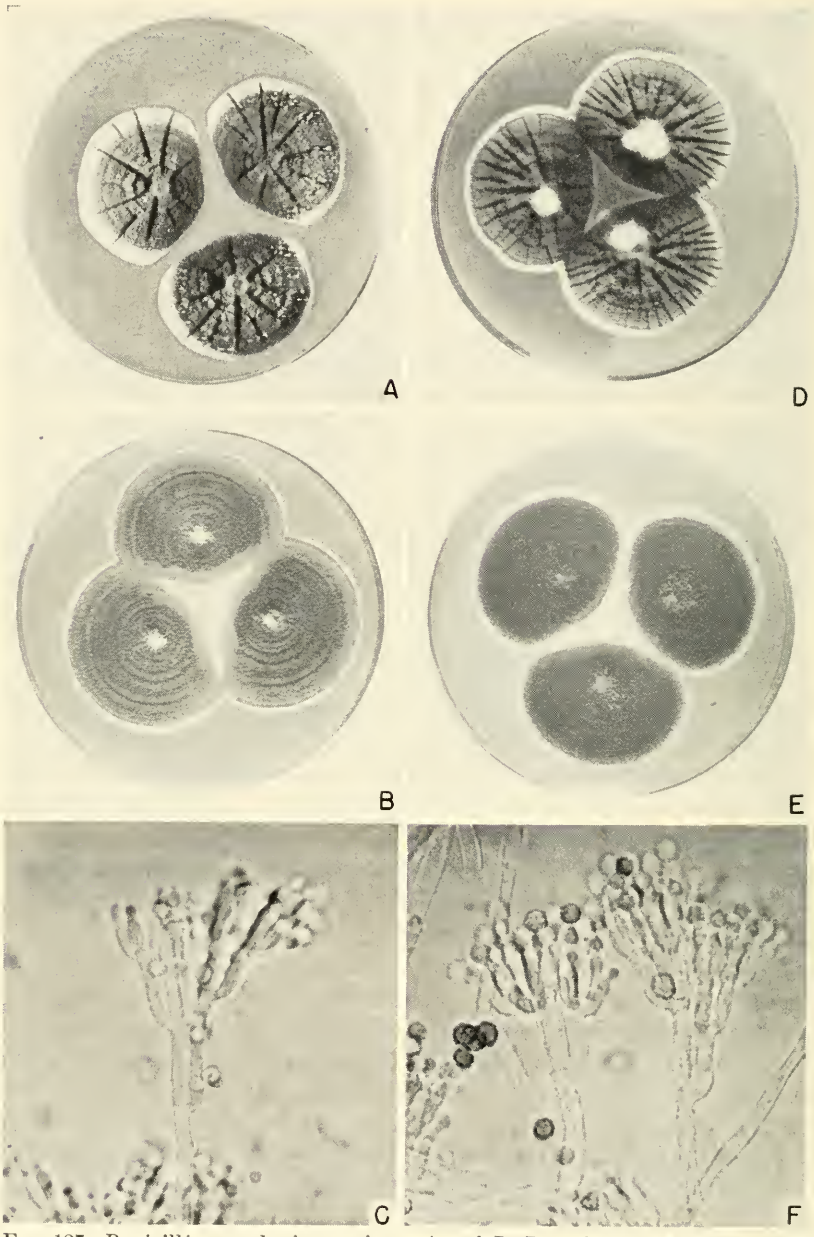


FIG. 127. *Penicillium cyclopium* series. *A* and *B*, *P. cyclopium* Westling, NRRL 1899, on Czapek and malt agars at 10 days. *C*, Detail of penicillus, showing conidia smooth or nearly so, × 750. *D* and *E*, *P. cyclopium* West. var. *echinulatum* n. var., NRRL 1151, on Czapek and malt agars at 10 days. *F*, Detail of penicilli showing conspicuously roughened conidia, × 750.

pearing granular or "mealy", conidiophores arising from the substratum, often crowded into fascicles or tufts, but usually borne more or less separately; exudate lacking in some strains, abundantly produced in others, clear or very faintly colored in pink or orange shades; odor pronounced, "moldy" but difficult to characterize; reverse uncolored or yellowish at first, becoming orange-brown or even purplish in two weeks in most strains, remaining essentially colorless in others; penicilli large, about 50 to 60μ in length, asymmetrically branched, bearing tangled chains of conidia in irregular masses up to 150μ long (fig. 126A); conidiophores arising from the substratum, mostly 200 to 400μ in length by 3.0 to 3.5μ in diameter, sometimes coarser, with walls typically roughened but in some strains appearing smooth or nearly so; penicillus usually showing one or occasionally more branches, 15 to 30μ by 2.5 to 3.5μ, often appressed and like the main axis usually bearing 3 to 4 metulae 10 to 15μ by 2.5 to 3.3μ (figs. 126B and 127C), each supporting a verticil of 4 to 8 sterigmata measuring 7 to 10μ by 2.2 to 2.8μ, with apices ending abruptly in conidial chains; conidia mostly subglobose 3.5 to 4.0μ in diameter but with both globose and elliptical conidia observed, the latter commonly ranging from 3.3 to 4.0μ by 2.5 to 3.0μ, with walls smooth or delicately roughened.

Colonies on steep agar growing more rapidly than on Czapek, usually 6.0 to 6.5 cm. in diameter in 12 days, commonly heavily sporing but in general reproducing the colony pattern described above; penicilli as described on Czapek but with conidiophore walls often more definitely roughened.

Colonies on malt agar spreading broadly, attaining a diameter of 6.5 to 7.0 cm. in 12 days, plane or nearly so, appearing more or less granular, not furrowed but often showing concentric zones of clustered (fascicles) conidiophores (fig. 127B); penicilli as on Czapek agar; walls of conidiophores more coarsely roughened and this roughening often extending to the metulae; conidial chains commonly up to 200μ or more in length.

Species description based upon the detailed comparative examination of more than a score of strains grown in agar plate cultures for the present study. Since the description is drawn in very broad terms, no single strain can be cited as wholly typical. However, the following cultures may be regarded as representative of *Penicillium cyclopium*: NRRL 942, from the Thom Collection as No. 4733.48, received originally from Biourge and regarded by both Thom and Biourge as representing this species; NRRL 1899 received from Professor H. W. Florey as No. M-22, capable of producing an antibiotic (subsequently identified as penicillic acid) that inhibited *Staphylococcus* species and *Escherichia coli*; NRRL 941 from the Thom Collection as No. 4733.43, received originally from Biourge as *P. corymbiferum* Westling but regarded by Thom (1930, p. 385) as representing *P. cyclopium;*

and NRRL 1888 from George Smith, London School of Hygiene and Tropical Medicine, as their No. 123, a culture of *P. cyclopium* found by Raistrick and associates (1936) to produce penicillic acid.

Penicillium cyclopium is reported from many different substrata and is world-wide in distribution. It has appeared in Holland and in the United States as the dominant mold in rotting bulbs belonging to the lily family, attacking and destroying the growing point. It is among the more common forms submitted for identification by collaborators and has been isolated from various types of ripe or aging fruit, grain and cereal products, soil and decaying vegetation, bee hives, mildewing tentage, etc. As described above, the species embraces a wide range of isolates or strains which vary one from another in particular cultural or microscopic details, yet are characterized by their "granular colonies" of rather dull blue-green color, finely roughened conidiophores (on Czapek agar), and predominantly subglobose spores.

Penicillium conditaneum Westling (Arkiv för Botanik **11**: 52, 63–65, figs. 46 and 2. 1911) was isolated from *Ribes nigra* and described in terms which ally it with *P. cyclopium* Westling as indicated by Thom's placement of the species in his Monograph (1930). Unfortunately the type strain has been lost from collections, and there was no material available for this study that could be regarded as representing with certainty Westling's concept of his species. Re-examination of Thom's notes on Westling's type strain (Thom No. 2538) leads us to believe that *P. conditaneum* hardly represented more than a strain difference. This species is, therefore, regarded as a probable synonym of *P. cyclopium*, which is rather generally recognized.

Penicillium aurantio-griseum Dierckx (Soc. Scien. Bruxelles **25**: 88. 1901. See Biourge, Monogr., La Cellule **33**: 126–128; Col. Pl. I and Pl. II, fig. 8. 1923) was described by Biourge in terms which place it with *P. cyclopium* as this species is considered here. Examination of the type strain, NRRL 971 (Thom No. 4733.7), in the present study confirms such placement. Colonies are somewhat restricted, 2.0 to 2.5 cm. in 10 to 12 days, but otherwise typical of the series. Conidia are more consistently elliptical than in such typical strains of *P. cyclopium* as NRRL 1888 and 1899 (see above), hence more nearly approach *P. martensii*. Other characters more nearly duplicate those of *P. cyclopium*. We believe *P. aurantio-griseum* Dierckx should be regarded as a member of the *P. cyclopium* series but showing insufficient strain individuality to warrant continued species recognition.

Penicillium aurantio-griseum Dierckx var. *poznaniensis* Zaleski (in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 444–445, Taf. 37. 1927), as known by a strain received from Zaleski under this name, represents a member of the *P. cyclopium* series approximating the species *P. cyclopium* Westling except colonies are hardly fasciculate upon any culture medium. The strain produces strong earthy odors characteristic of the species; conidiophores are rough-walled, and penicilli commonly show a rather compact branching system. This latter character led Thom (1930, pp. 301–302) to place the variety in the *P. brevi-compactum* series. Other considerations, however, seem to outweigh this, and the form is believed to be more correctly placed in the Fasciculata.

Penicillium bordzilowskii Morotchkovsky (Bul. Sci. Rec. Biol. Univ. Kiev **2**: 71, fig. 2. 1936) was described in terms which seem to relate it to *P. cyclopium* Westling. The type has not been seen. A translation of the latin diagnosis follows: Colonies at first white, then dark cinereus gray, at length gray-green, irregularly radiate with margin narrow, sterile, white; reverse yellowish, unevenly radiate; conidiophores smooth, erect, septate, 4.0 to 5.5μ in diameter, branched; branches 24 to 27.2μ by 4.5 to 5.0μ mostly in three's, somewhat thickened toward the apex; metulae mostly in three's or four's, 10.8 to 13.6μ by 3.5 to 3.0μ, a little thickened toward the apex; sterigmata in three's or four's, fusiform 10.8 to 13.6μ by 2.5 to 2.8μ; conidia globose, 2.5 to 2.8μ in diameter, smooth, in chains without connectives; coremia dense, stipes white, 800 to 850μ in height; sterile hyphae anastomosing. Colonies quickly liquifying 15 per cent gelatin. Habitat: On roots of rotting sugar beets in the Ukraine.

Penicillium cyclopium Westling var. **echinulatum** n. var.

Colonies on Czapek's solution agar essentially duplicating those of the species in rate of growth, conidial color, texture (fig. 127D), and colors in reverse; exudate abundant, clear; penicilli large, up to 50μ or more in length, commonly twice or even three-times branched, in general duplicating those of the species (fig. 127F); conidiophore walls often granular; metulae and sterigmata as in the species; conidia globose to subglobose, 3.5 to 4.5μ, occasionally larger, with walls comparatively heavy and conspicuously rough-echinulate, dark green in mass.

Colonies on steep and malt agars (fig. 127E) not differing significantly from those of the species, but with conidia of the variety when grown upon malt agar even more conspicuously echinulate than when cultivated on Czapek.

Varietal description based on NRRL 1151, received in 1940, from G. A. Ledingham, National Research Council, Ottawa, Canada, as an isolate from a contaminated agar plate. Represented also by NRRL 1153 from the same source, differing only in producing colonies less definitely blue-green, near sage green (Ridgway, Pl. XLVII).

The variety differs from the species primarily in the roughness of its conidia, upon which character the varietal name is based.

Penicillium puberulum Bainier, in Bul. Soc. Mycol. France **23**: 16–17; Pl. IV, figs. 6–12. 1907. See also Thom in Alsberg and Black, U.S.D.A., Bur. Plant Ind., Bul. 270: pp. 12–13. 1913; and Thom, The Penicillia, pp. 271–272, figs. 36 and 37. 1930.

Colonies on Czapek's solution agar growing more or less restrictedly, attaining a diameter of 3.0 to 3.5 cm. in 2 weeks at room temperature, with surface velvety to somewhat granular, raised and occasionally almost umbonate in central areas, with submarginal areas radiately wrinkled, azonate during the rapidly growing period but becoming more or less zonate in age and often showing a thin, spreading marginal area up to 1 cm. in width,

closely but delicately zonate; growing margin white to light gray-green, 1 mm wide, quickly becoming darker, fruiting areas at first bluish green near gnaphalium green but shading quickly to slate olive (Ridgway, Pl. XLVII) and finally to dark olive-gray (R., Pl. LII), at 2 to 3 weeks commonly showing an area of submerged growth up to 2 mm. wide surrounding the colony and bearing scattered penicilli; reverse yellowish to tan to almost brownish black in colony center, with surrounding agar uncolored; exudate lacking or limited in amount, colorless; odor moldy to sourish, strong; conidiophores arising primarily from a tough basal mycelial felt, generally less than 200μ in length by 3.5 to 4.0μ wide, slightly sinuous with walls more or less roughened; penicilli asymmetric, consisting of a terminal verticil of metulae or of such a verticil with branches and metulae arising from a lower node, often irregularly branched; branches usually 10 to 20μ by 2.8 to 3.5μ; metulae usually in groups of 2 to 4, ranging in dimensions from 9.0 to 15μ by 2.5 to 3.5μ; sterigmata usually in groups of 3 to 5 and measuring 7.0 to 9.0μ by 2.5 to 3.5μ, with form not distinctive, conidia globose to subglobose, with walls smooth or delicately roughened, mostly 3.0 to 3.5μ in diameter but variable in size up to 5.0 to 5.5μ.

Colonies on steep agar growing more rapidly, attaining a diameter of 4.0 to 4.5 cm. in 2 weeks at room temperature, essentially similar in pattern and coloration to the above, and producing penicilli as described.

Colonies on malt extract agar attaining a diameter of 5.5 to 6.0 cm. in 2 weeks at room temperature, with colony center raised, loose-textured, with sub-marginal area sometimes lightly furrowed in a radial pattern, ranging from almost non-sporulating to heavily sporing depending upon the strain, and with marginal zone up to 1.5 cm. sometimes plane, conidial areas in lighter blue-green shades than on Czapek, ranging from gnaphalium green to pea green (R., Pl. XLVII); penicilli essentially as on Czapek but with conidiophores more consistently roughened.

Penicillium puberulum Bainier is occasionally isolated from soil, from decaying vegetation, and from stored cereal grains.

Species description based upon Thom's diagnosis as furnished to and published by Alsberg and Black (1913) and as republished by Thom in his Monograph (1930), together with our current observations on cultures from the same original source. One of these, NRRL 2040, was received from the Centraalbureau in May 1946 and represents a culture sent to Professor Westerdijk immediately after the publication of Alsberg and Black's work. This strain was isolated from *Zea Mays* prior to 1913. Another culture, NRRL 1889, was received in August 1942 from George Smith, London School of Hygiene and Tropical Medicine, as No. Ad 113 with the accompanying notation: "Obtained by Dr. Birkinshaw from Dr. Thom in 1928 as No. 4876.20—it appears to be typical." As noted by

Thom in The Penicillia (1930, p. 272), this latter number represented the culture studied by Alsberg and Black. The two subcultures remain identical.

A third culture, NRRL 845, stemming from the same original source, was received by us in 1935 from George Smith as No. Ad 31, and at that time duplicated the typical cultural picture. Some variation has taken place during the ensuing years, and today NRRL 845 when grown on Czapek agar produces colonies that are somewhat looser in texture, and generally lighter sporing than is typical of the species. On steep agar the degree of variation is even more pronounced and colonies commonly show abundant vegetative mycelium in shades near pale vinaceous fawn (Ridgway, Pl. XL) to venetian pink (R., Pl. XIII) with conidial areas ranging through gnaphalium green or pea green to dark olive gray (R., Pl. XLVII) in age. The penicilli, although often somewhat irregular in form, may be regarded as representative of the species as described above. In cultural appearance strain NRRL 845, as it exists today, suggests *Penicillium commune* Thom (NRRL 890) in the Lanata section.

The proper taxonomic position of *Penicillium puberulum* remains in doubt. Thom (1930) placed it in his Asymmetrica-Velutina section, and based this placement upon the production of colonies that were essentially velvety. This character remains unaltered, except for the development of limited fasciculate structures in older colonies. The species shows additional evidence of relationship to the *P. cyclopium* series, since penicilli are commonly branched, conidiophore walls are roughened, and a strong moldy odor characteristic of many members of the *P. cyclopium* series is regularly produced. Furthermore, the production of penicillic acid by *P. cyclopium* Westling (Birkinshaw, Oxford, and Raistrick, 1931) as well as *P. puberulum*, from which it was first identified (Alsberg and Black, 1913), may indicate a relationship to the Fasciculata. While the production of similar or related metabolic products must not be accepted as proof of relationship *per se*, it often provides useful clues to such relationship.

Penicillium majusculum Westling (Arkiv för Botanik **11:** 51–52, 60–62, figs. 1 and 45. 1911) is believed to represent a synonym of *P. puberulum* Bainier. Review of Thom's notes (1930, pp. 389–390) made on a culture received from Westling as his type fails to reveal either cultural or microscopical differences which would warrant separation of the two species. Examination of this culture, NRRL 954, and a culture from Biourge, NRRL 955, bearing this same name (presumably derived from Westling's type through Thom), shows the two to be identical and to agree very closely in cultural aspect and in structural detail with NRRL 1889 and 2040. The name *P. puberulum* Bainier is retained because the culture received from Westling under the name *P. majusculum* never agreed very closely with his original description (see Thom, 1930, p. 390), and because a considerable mass of biochemical literature has been built up around the use of the name *P. puberulum* Bainier.

Penicillium porraceum Biourge (in Monogr., La Cellule **33**: fasc. 1, pp. 188–189; Col. Pl. V and Pl. IX, fig. 49. 1923) is believed to represent a member of the *P. cyclopium* series, assignable most satisfactorily with *P. puberulum* Bainier. Biourge regarded the species as belonging with *P. stoloniferum* Thom. Basing his conclusions on subsequent study of Biourge's culture (Thom No. 4733.98—now maintained as NRRL 970), Thom questioned this relationship and placed the species in the Fasciculata. Re-examination of this culture confirms this placement and leads us to regard it as belonging in the *P. cyclopium* series. It is placed with *P. puberulum* because of its somewhat restricted growth and comparatively small penicilli.

Penicillium pezizoides (Biourge) nomen nudum. A culture bearing this name was received from Biourge in 1934, but apparently was never described. The strain as received, and as now maintained in our Collection (NRRL 987), produces colonies 0.5 to 1.0 mm. deep, with vegetative mycelium in light pink shades and characterized by numerous pink, *Peziza*-like craters that result from the evaporation of large droplets of exudate partially embedded in the mycelial felt; conidia are in bluish glaucous shades; conidiophores are rough-walled, arise from the substratum, and are commonly aggregated into fascicles; penicilli are asymmetric and irregularly branched. Except for the regular development of *Peziza*-like craters, a tendency that is often seen on a lesser scale in other strains and species, there is little to distinguish Biourge's strain from *P. puberulum* as represented by NRRL 845.

Penicillium martensii Biourge, in Monograph, La Cellule **33**: fasc. 1, pp. 152–154; Col. Pl. II and Pl. III, fig. 14. 1923. Thom, The Penicillia, pp. 388–389. 1930.

Colonies on Czapek's solution agar (Col. Pl. VIII and fig. 128A) growing fairly rapidly, attaining a diameter of 4.0 to 4.5 cm. in 12 to 14 days at room temperature, with central areas commonly raised, and usually marked by radial furrows, but in some strains remaining essentially plane, with growing margins 1 to 2 mm. wide, white, with marginal areas narrowly but definitely zonate in most strains, and with surface appearing granular to definitely tufted, heavily sporing throughout, shading from glaucous blue shades (Ridgway, Pl. XLII) in young conidial areas through bluish gray-green shades to dark bluish gray-green (R., Pl. XLII) lily green (R., Pl. XLVII) or grayish blue-green (R., Pl. XLVIII) at maturity and usually becoming dull gray in age; exudate limited or abundantly produced, clear; odor often pronounced, moldy; colonies in reverse at first lightly colored, becoming orange-brown to light maroon, and sometimes showing a purplish shade in age, with the surrounding agar becoming similarly colored in most strains; penicilli comparatively large, mostly 40 to 50μ in length bearing conidia in tangled chains, forming rather irregular masses up to 150 to 200μ in length; conidiophores arising directly from the substratum, variable in length (especially in different strains) but commonly ranging from 200 to 400μ by 3.0 to 3.5μ, with walls generally smooth or in some strains slightly roughened; penicilli usually showing one or two branches, mostly 15 to 20μ by 3.0 to 3.5μ, in addition to the main axis (fig. 128C),

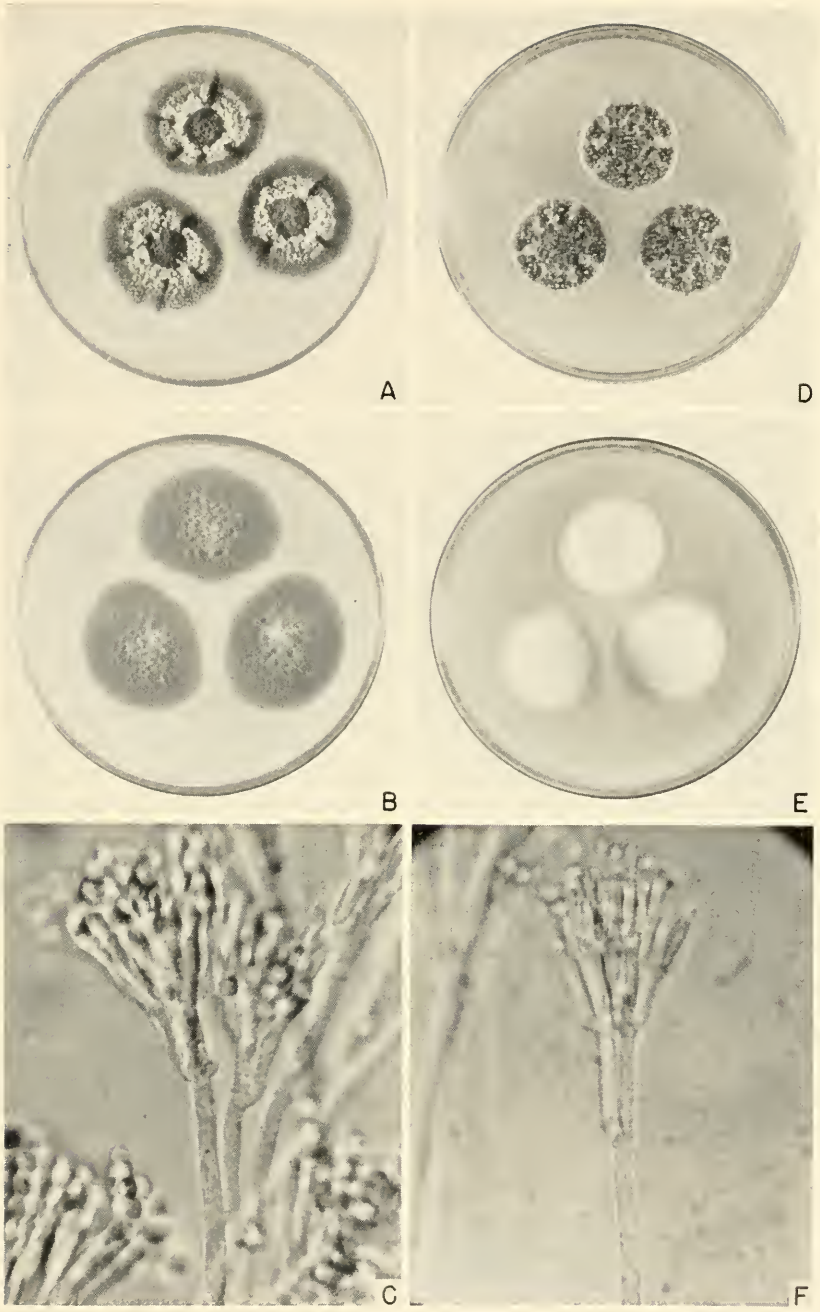


FIG. 128. *Penicillium cyclopium* series (continued). *A* and *B*, *P. martensii* Biourge, NRRL 2027, on Czapek and malt agars at 10 days. *C*, Detail of the penicillus, × 1000. *D* and *E*, *P. aurantio-virens* Biourge, NRRL 2138, on Czapek and malt agars at 10 days. *F*, Detail of the penicillus, × 750.

often but not consistently appressed; metulae commonly 3 to 5 in the verticil, about 10 to 12μ by 2.5 to 3.0μ; sterigmata usually in clusters of 4 to 8, measuring 7 to 9 by 2.0 to 2.5μ with apices somewhat narrowed; conidia smooth-walled, elliptical to subglobose, mostly 3.3 to 4.0μ by 3.0 to 3.3μ but occasionally up to 5.0 to 5.5μ by 3.0 to 4.0μ.

Colonies on steep agar growing somewhat more rapidly than on Czapek but in general showing essentially the same cultural characteristics, often more closely and less deeply furrowed, heavy sporing throughout and colored as described above; odor pronounced, moldy, in age sourish; abundant clear exudate often produced; reverse commonly showing vinaceous purple shades in central colony areas; penicilli essentially as on Czapek but with conidia showing greater variability in size and form.

Colonies on malt agar spreading (fig. 128B), essentially plane, in some strains narrowly to conspicuously zonate, with fasciculation fairly pronounced, in others appearing almost velvety, generally heavy sporing; no exudate; reverse in rich orange-brown shades; penicilli mostly as on Czapek but with conidiophores and branches more definitely roughened.

Species description based upon comparative cultural and microscopical examinations of numerous strains, of which NRRL 2027 and NRRL 956 may be regarded as typical. The former was isolated at Baarn in 1943 and received from the Centraalbureau in April 1946 as *Penicillium martensii* Biourge. The latter was obtained from the Thom collection as No. 5010.11, and was originally received as Zaleski's type strain of *P. johannioli* Zaleski (see below). Other strains representing the species include: NRRL 951, from the Thom Collection as No. 4733.77, (Biourge's No. 82) and presumably the type for *P. janthogenum* Biourge (see below); and NRRL 2030, a strain isolated from tent lines in the South Pacific area in 1944, subsequently submitted to us for identification.

Cultures of *Penicillium martensii* seem to be unusually subject to variation when long maintained in continued culture. It is unfortunate that Biourge's type, NRRL 952 (Thom's No. 4733.87), has become so definitely floccose and atypical that it can no longer be regarded as representative of the species. Years of study and the repeated assignment of newly isolated strains to this species, however, have tended to establish as typical, the characteristics shown by the strains cited above.

Penicillium martensii Biourge of this Manual is described in broad enough terms to include a variety of strains, or isolates, differing from each other in particular characteristics. All, however, possess certain characters in common, to-wit: colonies are definitely *blue*-green with the blue element conspicuously pronounced; colonies in reverse commonly show a vinaceous or purplish coloration; conidiophores upon Czapek's solution agar are smooth or nearly so (but, as is characteristic of almost

all the Fasciculata, are rough on malt agar); and conidia are generally elliptical to subglobose and smooth-walled.

Penicillium janthogenum Biourge (Monograph, La Cellule **33:** fasc. 1, pp. 143–145; Col. Pl. II and Pl. III, fig. 13. 1923) may likewise be regarded as synonymous with *P. martensii* since careful examinations of original descriptions and figures fails to reveal any significant differences between the two. Close similarity of these forms was observed by Thom (1930) who studied the type material of both species. Careful examination of NRRL 951 (from the Thom Collection as No. 4733.77), representing Biourge's type of *P. janthog num*, in our current study confirms the authenticity of the culture, yet fails to reveal any marked differences between this strain and other isolates regarded as typical of *P. martensii* Biourge.

A strain, NRRL 2034, received from the Centraalbureau as *P. janthogenum* Biourge, contributed by Rennerfelt in 1936, produces penicilli usually with one closely appressed branch, consistently elliptical conidia, and smooth-walled conidiophores on all media. It does not differ significantly from *P. martensii*.

Penicillium johannioli Zaleski (Bul. Acad. Polon. Sci.: Math. et Nat. Ser. B, pp. 453–454; Taf. 40. 1927) was described in terms which clearly align it with *P. martensii* as previously published by Biourge. In Thom's Monograph (1930) both species were included and minor differences in zonation and depth of colonies, colony color in reverse, character of stalk walls, etc., may be noted in the descriptions given. After careful consideration, we are led to believe that *P. johannioli* represents, at most, a somewhat divergent example of a variable species. NRRL 965, the type strain of *P. johannioli* differs from the more commonplace strains of *P. martensii* by producing an unusual amount of clear exudate and conidia that are more definitely and persistently elliptical. The rich blue-green color of both species has been reported by their authors. The species is regarded as synonymous with Biourge's prior species *P. martensii*.

Penicillium polonicum Zaleski (Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 445–447, Taf. 38. 1927) was placed near *P. patulum* Bainier by Thom (1930) primarily on the bases of its elliptical conidia and its bluish green to gray color (in age). Careful study of the type strain, NRRL 995, as maintained in our collection and as received from the Centraalbureau in May 1946, leads us to question this placement. These strains differ from *P. urticae* in producing colonies with more blue coloration, conidiophore walls slightly roughened on Czapek and definitely roughened on malt, sterigmata and metulae consistently longer, and pronounced moldy odors. These characteristics clearly align the cultures with the *P. cyclopium* series. Assignment to a specific species is not recommended, but the existing cultures, the original description, and Thom's notes (1930) indicate closer relationship to *P. martensii* Biourge than to *P. cyclopium* Westling.

Penicillium aurantio-virens Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 119–121; Col. Pl. I and Pl. I, fig. 5. 1923. Thom, The Penicillia, pp. 316–317. 1930.

Colonies on Czapek's solution agar (fig. 128D) attaining a diameter of 2.5 to 3.0 cm. in 10 days at room temperature, in some strains growing irregularly with some areas or sectors restricted and strongly tufted and others spreading and tending toward lanose or velvety, ranging from 500μ

to 1 mm. or more deep, in other strains thinner and usually showing numerous radial lines which first appear as furrows but subsequently develop as ridges due to secondary growth, zonate with margins white, shading from celandine green to lily green (Ridgway, Pl. XLVII) or deep bluish gray-green (R., Pl. XLII) in areas of mature penicilli; odor strong, "moldy"; exudate limited, colorless to very pale yellow; reverse in orange-red shades with surrounding agar becoming similarly colored, sometimes as a conspicuous halo 1 to 2 cm. beyond the colony margin; sporulating abundantly with conidiophores arising from the substratum or as branches from aerial hyphae, commonly 200 to 300μ by 3.0 to 3.5μ, occasionally longer, with walls finely roughened, bearing conidial structures of intermediate size characterized by tangled conidial chains; penicilli biverticillate and asymmetric (fig. 128F), irregularly branched with metulae and sterigmata commonly borne at different levels; branches variable in size, commonly 10 to 15μ by 2.5 to 3.0μ, occasionally longer; metulae usually in clusters of 2 to 4, commonly 10 to 12μ by 2.5 to 3.0μ; sterigmata usually 6.5 to 8.0μ by 2.0 to 2.5μ, sometimes longer with abnormal cells occasionally observed, tending to become detached in mounts of older structures; conidia elliptical to subglobose, commonly measuring 3.0 to 3.5 or even 4.0μ in long axis, smooth-walled.

Colonies on steep agar grow more rapidly and are more closely and conspicuously ridged than on Czapek, about 3.5 to 4.0 cm. in diameter in 10 days at room temperature, lanose to tufted-fasciculate, 1.0 to 1.5 mm. deep, heavily sporulating; exudate limited, colorless, largely embedded in the mycelium; colony reverse in dull orange to maroon shades with agar similarly colored in surrounding zones up to 1 to 2 cm. in width; penicilli generally larger with branches longer and more numerous than on Czapek, but otherwise similar.

Colonies on malt agar about 3.0 to 3.5 cm. in diameter in 10 to 12 days, consisting of a basal felt bearing a loose, floccose surface growth ranging from thin in the marginal area to 1 to 2 mm. deep in colony centers, pale yellow in color and usually non-sporulating (fig. 128E); no exudate; reverse in orange shades with surrounding agar colored in bay shades, sometimes to a distance of 2 cm.

The species is represented by NRRL 2138 received from George Smith, London School of Hygiene and Tropical Medicine in June 1947 as a subculture derived from the original type. NRRL 2010 and NRRL 881, obtained from the Centraalbureau and from the Thom Collection respectively as Biourge's *Penicillium aurantio-virens*, are also representative of the species, but differ from the above in being more nearly velvety and, therefore, less typical of the group to which the species is assigned. NRRL 2029, isolated at this Laboratory from spoiled starch paste supplied by

Mary J. Cox, represents a heavily sporing and strongly fasciculate strain. The species is regarded as closely related to *P. martensii* of the same author.

Penicillium aurantio-virens is characterized particularly by its reduced sporulation upon malt agar, by the production of conspicuous halos of diffusible orange-red pigment in the agar surrounding the growing culture, and by the yellow coloration of its vegetative mycelium, particularly upon malt agar.

Penicillium brunneo-violaceum Biourge (Monogr., La Cellule **33**: fasc. 1, pp. 145–147, Col. Pl. II and Pl. IV, fig. 21. 1923) as known from Biourge's description and type culture received from the Centraalbureau in February, 1946, and now maintained as NRRL 2137, represents a form approximating *P. aurantio-virens* Biourge in cultural and structural details. Thom, in 1930, placed this species in the Fasciculata upon the basis of small tufts of conidiophores. Such structures are commonly observed in *P. aurantio-virens* and constitute the primary basis for transferring this species from the Lanata (where Thom assigned it in 1930) to the Fasciculata.

Penicillium flavido-marginatum Biourge (Monogr., La Cellule **33**: fasc. 1, pp. 150–152; Col. Pl. III and Pl. IV, fig. 24. 1923) was described in terms which seem to relate it to *P. aurantio-virens* of the same author. Thom's notes, made from Biourge's type, in general confirm such relationship (1930, pp. 315–316). Re-examination of this culture, now maintained as NRRL 880, shows penicilli appearing mostly monoverticillate or as fragmentary biverticillate-asymmetric structures. The culture can no longer be regarded as satisfactorily representing Biourge's species. A culture bearing this name, received from the Centraalbureau in March 1946, is lighter sporing and equally unsatisfactory as type material.

Occurrence and Significance

Penicillium cyclopium Westling and *P. martensii* Biourge appear to be world-wide in distribution and to be fairly omnivorous in the substrata upon which they grow. They are frequently isolated from stored grain and various cereal products. They are often encountered growing upon pomaceous and stone fruits as a secondary rather than a primary parasite. They are not infrequently encountered in soil platings, and they have appeared several times among the molds isolated from deteriorating military equipment in both temperate and tropical areas. *Penicillium puberulum* Bainier and *P. aurantio-virens* Biourge are apparently less common in nature, but apparently occur upon similar substrata.

Members of the series are quite active biochemically. Alsberg and Black (1913), studying the possible relation between pellagra and moldy maize, succeeded in isolating from a *Penicillium*, identified by Thom as *Penicillium puberulum* Bainier, an undescribed metabolic product which they named penicillic acid, $C_8H_{10}O_4$. Its toxic character was demonstrated and its properties described but its constitution was not determined. Raulin's medium, modified in different ways, was used as a substrate.

Almost 20 years later Birkinshaw and Raistrick (1932) re-examined the

culture previously studied by Alsberg and Black and found it to produce from glucose two new metabolic products in addition to penicillic acid, which was also formed but in reduced yield. For one of these, having the empirical formula $C_8H_6O_6$, they proposed the name "puberulic acid," whereas the other was referred to as acid $C_8H_4O_6$. *Penicillium aurantiovirens* (Biourge's type strain) also was investigated and found to produce greater quantities of both puberulic acid and acid $C_8H_4O_6$ than the strain of *P. puberulum* from which these compounds were first identified. Puberulic acid was found to be a practically colorless dibasic acid (M.P. 316–318°C.), and to give a purple-brown color with $FeCl_3$. It was thought to possibly form an oxidation-reduction system with acid $C_8H_4O_6$. Barger and Dorrer (1934) investigated further the production of puberulic acid and acid $C_8H_4O_6$, which they referred to as a "yellow acid." Methods of obtaining increased yields together with additional information regarding the chemical properties of the two acids were reported. Oxford, Raistrick, and Smith (1942b) investigated the antibacterial properties of puberulic acid and the hitherto unnamed yellow acid, $C_8H_4O_6$, for which they proposed the name puberulonic acid. The latter is characterized by bright yellow prisms, M.P. 298°C., and upon neutralization undergoes a series of curious color changes (also noted by Barger and Dorrer, 1934). Various species of bacteria were inhibited by both acids in fairly low concentration, with puberulic generally the more potent. Both were generally more effective against cocci than against the various Gram-negative forms tested. Strains of *P. johannioli* Zaleski (= *P. martensii* Biourge of this Manual) were most productive of puberulonic acid.

The biochemistry of *Penicillium puberulum* was re-examined by Birkinshaw, Oxford, and Raistrick in 1936, with special reference to the production, study, and characterization of penicillic acid. A culture of *P. cyclopium* from Baarn (derived from Westling's original strain) was found to produce considerably greater yields than the Alsberg and Black strain of *P. puberulum* as then maintained in laboratory culture. Penicillic acid was reported to be slightly soluble in cold water and readily soluble in hot water, ether, alcohol, benzene, and chloroform; it crystallized as needles (M.P. 83–84°C.); gave no color with $FeCl_3$ in the cold but turned orange-brown upon warming. It was optically inactive. Whereas the production of penicillic acid is generally considered as characteristic of *P. puberulum* and related species of the Fasciculata, Karow, *et al.* (1944) reported its production also by *P. suavolens*, *P. thomii*, and *Aspergillus ochraceus*.

Alsberg and Black (1913) demonstrated the toxicity of penicillic acid. Its antibacterial properties were carefully investigated by Oxford, Raistrick, and Smith (1942a), who found the pure anhydrous acid to inhibit *Staphylococcus aureus* at a concentration of 1:50,000 to 1:100,000. Professor

Florey (personal communication) reported a *Penicillium*, subsequently identified by us as *Penicillium cyclopium* (NRRL 1899), to produce an antibiotic effective against *Staphylococcus*; the substance was later found to be penicillic acid. The mechanisms of antibiotic action of penicillic acid and clavacin were compared by Geiger and Conn (1945).

Birkinshaw, Callow, and Fischman (1931) demonstrated the production of ergosterol in the mycelium of *Penicillium puberulum* Bainier (Alsberg and Black's strain). A 0.13 per cent yield in the dried mycelium was reported in a typical experiment.

Anslow, Breen, and Raistrick (1940) reported the production of emodic acid, and the hitherto undescribed ω-hydroxyemodin from the mycelium of a culture reported to represent a strain of *Penicillium cyclopium* Westling. Emodic acid, $C_{15}H_8O_7$, M.P. 363–365°C., forms orange needles which are readily soluble in cold dilute sodium bicarbonate solution. ω-Hydroxyemodin, $C_{15}H_{10}O_6$, M.P. 288°C., forms dull orange needles, is insoluble in sodium bicarbonate solution but readily soluble in cold sodium carbonate. Based upon an exchange of material, ω-hydroxyemodin was found to be identical with an unnamed pigment isolated by Posternak (1939) from a culture reported as *P. citreo-roseum*.

Oxford and Raistrick (1935) isolated *i*-erythritol in small yields from both the mycelium and the metabolism solutions of strains of *Penicillium cyclopium* Westling and *P. brevi-compactum* Dierckx. The substance is readily soluble in cold water and occurred in greatest concentration in the early stages of growth. Some mannitol was likewise isolated from *P. cyclopium*.

Campbell, *et al.* (1945) isolated from the mycelium of *Penicillium puberulum* a photosensitive nitrogenous compound, $C_{17}H_{12}N_2O_2$, M.P. 220°C. (decompn.). It gave phenol upon heating, and *p*-hydroxybenzoic acid upon oxidation. The substance showed some antibiotic activity.

Semeniuk and Ball (1937) reported *Penicillium puberulum*, with members of the *P. notatum-chrysogenum* series, to be commonly isolated from meat in cold storage in Iowa. Morgan and Moir (1933), in New Zealand, found *P. puberulum* to be a chief cause of various types of discoloration in Cheddar cheese. Neill (1935), also working in New Zealand, reported *P. puberulum* to be a common mold on wooden boxes intended for shipment of butter. Control measures were discussed.

Penicillium cyclopium commonly causes a bulb rot in *Scilla*, *Lilium*, and other liliaceous plants. The disease is particularly severe when bulbs are stored at high temperatures and a high humidity (Singh, 1941). Infections generally enter through wounds but may develop from contact with diseased bulbs (Macfarlane, 1939). DuPlessis (1936) found *P. cyclopium* together with *P. expansum* and a form identified as *P. elongatum* to be

commonly associated with *Botrytis cinerea* Pers. on South African grapes intended for export. Burnside (1927) reported *P. cyclopium* to be one of several Penicillia, including *P. corylophilum*, *P. palitans*, *P. expansum*, *P. granulatum*, *P. chrysogenum*, and *P. commune*, to grow extensively on brood combs and on the dead bees remaining in the hives.

Demeter and Mossell (1932) reported *Penicillium brunneo-violaceum* Biourge (see p. 505) to cause a brown spotting of Camembert cheese. Control measures were discussed. Subsequently, Demeter and Pfundt (1936), investigating the nutrition of this *Penicillium* and the true Camembert mold, found that a 5 to 15 per cent concentration of NaCl depressed *P. brunneo-violaceum* more than *P. camemberti*. Glycine, cystine, albumin, and casein favored the Camembert mold; whereas leucine, glutamic acid, and peptone favored the objectional species.

Penicillium expansum Series
(Apple-rot Penicillia)

Outstanding Characters

Colonies usually spreading broadly, varying in depth depending upon the strain and the substratum, in dull yellow-green, gray-green, or glaucous shades, often definitely zonate, with zones showing abundant fascicles and intermediate areas showing mostly simple conidiophores, in some strains almost velvety throughout; regularly producing abundant conidia, sometimes in the form of crusts.

Conidiophores developing directly from the substratum, variable in length up to 750μ or more, comparatively coarse, with walls smooth to conspicuously roughened depending upon the species and strain, arising singly or in definite bundles or fascicles.

Penicilli asymmetric, comparatively large, commonly once or twice branched, with branches typically appressed against the main axis, and bearing metulae and sterigmata at approximately the same level, producing long, tangled chains of elliptical to subglobose conidia.

Reverse ranging from colorless or nearly so through yellow-brown shades to dark walnut brown.

Odor strong, moldy or earthy.

Typically cause a rapid and destructive rot in apples and other pomaceous fruits, commonly referred to as "blue-mold" rot.

Series Key

c. Colonies typically in dull yellow-green, gray-green or glaucous shades; conidiophores smooth or rough; responsible for destructive rot of pomaceous fru ts.
P. expansum series

1′. Conidiophores comparatively long, often up to 500μ or more in length, with walls smooth or finely roughened; conidia abundant but usually not forming definite crusts ..... *P. expansum* (Link) Thom

2′. Conidiophores usually shorter, with walls conspicuously roughened; conidia often forming definite crusts which break away when culture tube or dish is tapped ..... *P. crustosum* Thom

The present series is typified by one of the oldest and best known species of *Penicillium*, namely: *Penicillium expansum*. This species was described by Link in 1809 in his "Observationes," and with *P. glaucum* and *P. candidum* constituted the three species upon which Link established his genus *Penicillium*. He reported *P. expansum* to be common upon rotting fruits, which in Germany at that time probably represented mostly pomaceous types. There is every reason to believe that *P. expansum* as described by Link represents the species as we know it today. Having described *P. expansum*, and in some measure differentiated it from *P. glaucum* in 1809, Link in 1824 abandoned the species and referred all green Penicillia to *P. glaucum*. This practice has been followed all too generally to the present day, with the result that the name *P. glaucum* is now practically meaningless and almost any green *Penicillium* may be found referred to it.

Members of the *Penicillium expansum* series are not uncommon in or upon organic materials in contact with the soil. They occasionally occur upon grains and cereal products derived therefrom, including bread. They have been isolated from eggs and chickens in cold storage, and from the waste sulphite liquors of the wood pulp industry. They occasionally occur upon fabrics and other deteriorating military equipment. They are, however, most common and most characteristically isolated from ripe fruits, particularly apples and other pomaceous types, either in storage or as they reach the consumer-market. They typically produce a soft, brown rot that is highly destructive and which may spread rapidly through a storage area in the absence of adequate precautionary measures. Spores of the fungus are carried from the field on the surface of the fruit, and germinate and enter through cuts and abrasions in the cuticle and epidermis. Sizable areas of rot may develop before the mold reappears at the surface in the form of blue-green tufts of massed conidiophores, which often-times may be 2 to 3 mm. high and represent well defined coremia (fig. 130A).

When tested in the laboratory by piercing and inoculating sound apples, typical strains of *Penicillium expansum* will produce areas of rot from 3 to 4 cm. in diameter, extending inward to the core, within a period of 8 to 10 days (fig. 130B and C). Areas of green sporulation develop within two to three weeks at room temperature.

Penicillium crustosum Thom is also included in the present series, al-

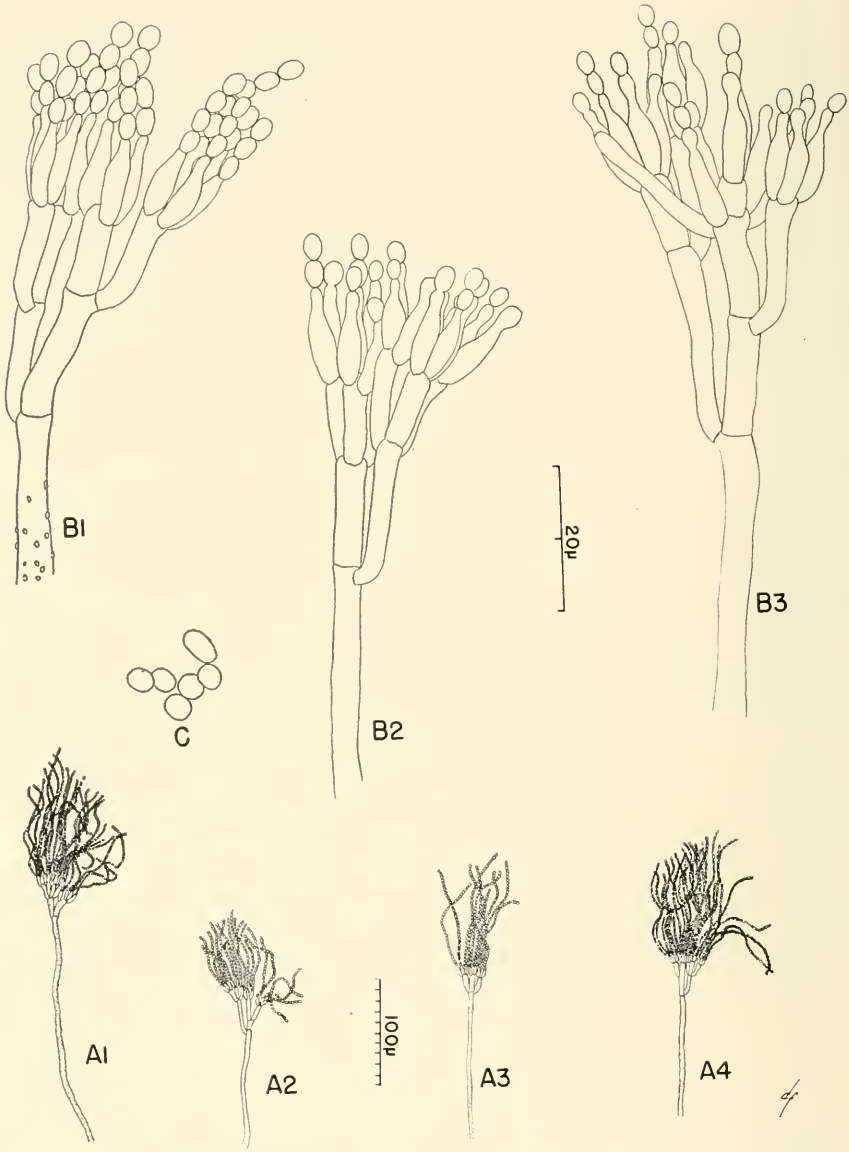


FIG. 129. *Penicillium expansum* Link. A_1–A_4, Habit sketches of representative penicilli. B_1–B_3, Detailed drawings of penicilli showing general pattern and arrangement of cellular elements. *C*, Mature conidia.

though it is much less common than *P. expansum* and typically produces a more limited rot of pomaceous fruits. It differs from the latter species in producing conidiophores that are usually somewhat shorter and are, as

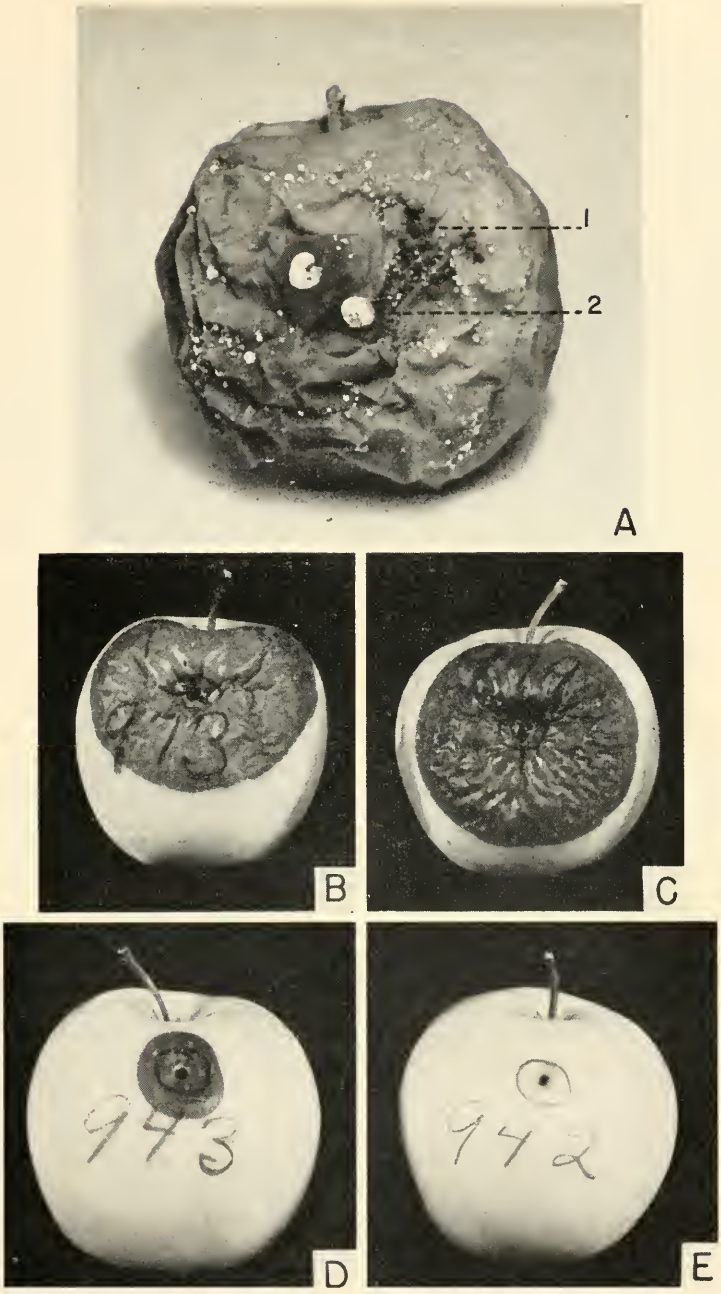


FIG. 130. Blue-mold rot of apples. *A*, Apple rotted by *Penicillium expansum* Link; note the dark, heavily sporing coremia (1) and the young larger coremia on which conidia are just beginning to develop (2). *B* and *C*, Apples (Grimes Golden) experimentally infected with strains of *P. expansum*, NRRL 973 and NRRL 979, respectively. *D*, Apple similarly infected with *P. crustosum*, NRRL 943, but showing reduced rot. *E*, Apple inoculated with but not infected by *P. cyclopium*, NRRL 942.

a rule, conspicuously roughened. Conidia are produced in great abundance, and in typical strains break off as irregular crusts or masses whenever the culture dish or tube is tapped (fig. 132). Like *P. expansum* it produces a strong moldy or earthy odor, and conidial areas are typically in the same dull yellow-green or glaucous shades. When inoculated into sound apples, typical strains of *P. crustosum* produce a limited rot (1.5 to 2.0 cm. in 7 to 10 days (fig. 130D)), but of the same general character as described above. This is in marked contrast to members of the *P. cyclopium* series (fig. 130E) and most members of the *P. viridicatum* series which produce no rot within two weeks when so inoculated.

Penicillium expansum Link, emended in Observationes, p. 17. 1809; Thom, in U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, pp. 27–28, fig. 1. 1910. See also Thom, The Penicillia, pp. 402–405, figs. 60 and 61. 1930.

Synonyms: *Coremium glaucum* Link, in Observationes, p. 19. 1809.
Floccaria glauca Greville, in Scottish Flora, Pl. 301, figs. 1–4. 1823–1828.
Penicillium glaucum Link (in part), in Species Plantarum VI: 70. 1824.
Coremium vulgare Corda (in part), in Prachtflora, p. 54, Pl. XXV, figs. 3, 4, 17–21. 1839.

Colonies on Czapek's solution agar growing rapidly (fig. 131A), attaining a diameter of 4 to 5 cm. in 8 to 10 days at room temperature, with surface generally showing radial furrows, often ranging from 0.5 to 2.0 mm. deep, heavily sporing throughout with conidiophores very abundant and regularly arising from the substratum, in some strains occurring in an almost continuous dense stand (fig. 131A), in others showing some definite fascicles or clusters but with the majority of the conidiophores arising singly, in still other strains with conidiophores almost entirely grouped into fascicles or bundles with colony surface appearing "mealy" to granular, marginal area 1 to 2 mm. wide, generally white during the growing period, shading quickly to yellow-green shades near celandine or sage green (Ridgway, Pl. XLVII) with the ripening of conidia; limited exudate produced, mostly in small droplets, partially embedded in the conidial mass, colorless; odor strong, "moldy", characteristic of rotting apples; reverse almost colorless in some strains through yellow-brown to deep walnut brown in others. Conidial structures very abundant and, in mass, characterizing the colony. Conidiophores mostly 150 to 400μ in length in some strains, but commonly up to 600 to 750μ in others, mostly 3.0 to 3.5μ in diameter with walls smooth or finely roughened, often appearing granular within, terminating in large penicilli commonly measuring up to 75 to 100μ in length, bearing long,

tangled chains of spores 150 to 200μ in length (fig. 129A); penicilli asymmetric, commonly once or twice branched, with branches mostly 15 to 25μ by 2.5 to 3.5μ, occasionally up to 50μ in length, typically appressed against the main axis with metulae arising from both at about the same level (fig.

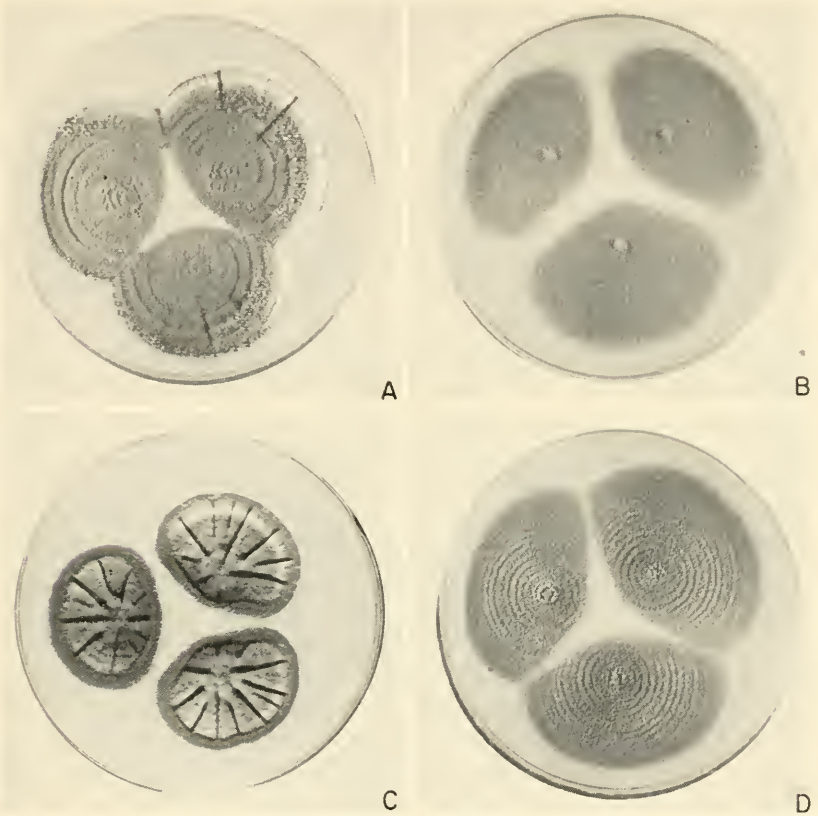


FIG. 131. *Penicillium expansum* series. *A* and *B*, *P. expansum* Link, NRRL 973, on Czapek and malt agars at 10 days. *C* and *D*, *P. crustosum* Thom, NRRL 1983, as the preceding.

129B); metulae usually borne in verticils of 3 to 6 and measuring about 10 to 15μ by 2.2 to 3.0μ; sterigmata in groups of 5 to 8 or 9 and usually ranging from 8 to 12μ by 2.0 to 2.5μ, occasionally up to 15 to 16μ by 3.0μ; conidia elliptical when first formed and usually continuing to show some ellipticity (fig. 129C), measuring mostly about 3.0 to 3.5μ in diameter, in some strains becoming almost globose at maturity with walls smooth, appearing dull yellow-green in mass.

Colonies on steep agar growing more rapidly than on Czapek, attaining

a diameter of 5.5 to 6.0 cm. in 8 to 10 days, essentially as described above in pattern and texture; penicilli generally larger and conidia commonly showing greater irregularity in dimensions.

Colonies on malt agar attaining a diameter of about 5 cm. in 8 to 10 days, plane (fig. 131B), comparatively thin, with surface appearing definitely mealy or granular, occasionally developing definite and fairly conspicuous coremia; conidiophores as on Czapek but often appearing rough in the area just above the agar surface, with penicilli essentially as on Czapek but with spore chains commonly up to 350μ in length.

Species description based upon such representative cultures as NRRL 973 (Thom No. 4189) isolated from apples in 1917 by Drs. J. S. Cooley and Charles Brooks, Bureau of Plant Industry; NRRL 976 (Thom No. 4852) isolated from apples by Dr. Cooley in 1926; and NRRL 977 (Thom No. 4933.1) isolated by Professor F. D. Heald. Of six strains received in February 1946 from the Centraalbureau under the name *Penicillium expansum*, three (labelled "from *Carica papaya*," "No. 10b," and "No. 37," respectively) duplicate NRRL 973; the others (labelled "v. Luijk α," "v. Luijk β," and "No. 35") duplicate NRRL 976. NRRL 979 (fig. 131C) cited in Thom's Monograph (1930, p. 412) as *P. clongatum* Dierckx from Professor A. W. Povah, as Thom's No. 5001.25, is regarded as representative of *P. expansum* (see p. 515).

Hundreds of strains belonging to this series have been isolated from naturally infected products. Workers in the fields of fruit storage and distribution find typical strains of *Penicillium expansum* to be the principal agent responsible for losses from storage rot. Coremia with white or more or less colored stalks and green heads composed of massed penicilli are abundantly observed on apples, pears, quinces and related fruits, also on grapes and cherries as they rot slowly in storage packages. Cultures from these penicillate heads produce the usual type of *P. expansum* already described, and conidia from these cultures regularly reproduce the rot found in the stored product which carried its infection from the field to the storehouse. Corda described and figured such coremia (Prachtflora, p. 54, Pl. XXV. 1839) as representing his species *Coremium vulgare*. Cultures from many coremia, as collected, clearly show that if such heads consist of massed penicillate fruits, the conidia from them will grow in ordinary culture media as Penicillia in which the coremiform nature of the species is represented by the more or less definite fasciculation of the conidiophores. Only rarely are large coremia comparable to those seen on fruit reproduced in agar cultures.

In handling rotting fruit and other material showing moldiness, numerous mycologists in different laboratories and at different times have isolated and described, or described directly from natural substrata, various species

which obviously represent the *Penicillium expansum* series. The number of species so described results both from the economic considerations underlying their isolation, and from the unusual prominence of these molds as they occur upon natural substrata in the form of yellow-green or glaucous, fasciculate or coremiform masses of fruiting structures. A partial list of such species follows while others are indicated among the synonyms of *P. expansum* Link already cited.

Coremium alphitopus Secretan, in Myc. Suisse III, pp. 539–540. 1833. Secretan described what he believed to be two varieties, A and B, and compared these with *Coremium leucopus* Persoon. The differences cited between the length and colors seen in the (coremium) stalks, and in the colors of the conidial heads have been seen many times in strains definitely belonging in the *Penicillium expansum* series as they develop upon various natural and laboratory media. Contrasts observed by the describer can be attributed to differences in the nutrient value of his substrata. We see no reason for separating either variety from *P. expansum* Link.

Penicillium crustaceum Fries, in Sys. Myc. **3**: 407. 1829. Fries went back to Linnaeus for a species name which the latter had used as *Mucor crustaceus*, although Greville in 1823 had already said that no one could identify *M. crustaceus*. Crusts of conidia consisting of adherent masses of spores formed from crowded penicilli are developed by strains in several series of the Penicillia, hence Fries' diagnosis is unspecific. He discussed his var. *β coremium*, as found upon fruits in autumn, as probably representing Persoon's *Coremium leucopus* and Greville's *Floccaria glauca*. Since these latter usages definitely refer to cultures now assignable to the *Penicillium expansum* series, it seems best to regard Fries' species as probably synonymous with *P. expansum* Link. In doing so, the possibility that it may represent *P. crustosum* Thom should not be overlooked. Exact identity cannot be established.

Penicillium glaucum Link *fide* Wehmer, in Beitr. z. Kennt. Einh. Pilze, II, p. 76–77; Taf. 1, fig. 5 and probably figs. 6 and 7; Taf. II, figs. 16–22. 1895. Wehmer's description indicates that he included in *P. glaucum* Link (1824 rather than 1809) forms which we regard as *P. expansum*. He distinguished the species by its more or less dark leaf green color (rarely blue-green) in contrast to the gray-blue or bluish gray, or brownish green of other species. Sclerotia were reported as rare and to measure from 100 to 800μ diameter.

Bainier (Bul. Soc. Mycol. France **21**: 126. 1905) referred to *Penicillium glaucum* as a coremium producing form "bien connues"—hence, in apparently the same sense as Wehmer.

Penicillium leucopus (Pers.) Biourge, in Compt. Rend. Soc. Biol. Paris **82**: 877–880. 1919; also Monogr., La Cellule **33**: pp. 107–111, Col. Pl. I and Pl. 1, fig. 1. 1923. Biourge's culture was received and clearly belonged in the *P. expansum* series. This usage simply raised the question whether we should base the accepted name upon Link (1809) or on Persoon's *Coremium leucopus* (Myc. European **1**: 42. 1822). We have followed Link.

Penicillium elongatum Dierckx, in Soc. Scientifique Bruxelles **25**: 87. 1901. Biourge put this species with *P. leucopus* (Pers.) Biourge, *P. expansum* Link of this book. Thom, in 1930, noted the persistent ellipticity of the conidia and recognized Dierckx's form as representing a type of mold occasionally isolated, but based sepa-

ration on conidial character only. Since bridging variations completely obliterate the distinctions then drawn, we may follow Biourge and drop this name.

Penicillium juglandis Weidemann, in Centbl. f. Bakt. etc., (II) **19**: 683–687, fig. 2. 1907. No worker has since reported Weidemann's organism, hence we are left to his description of a mold isolated from a walnut. Weidemann found his organism tolerant of 25 percent tannin in the culture solution, and to produce oxalic acid. Biourge placed it in his *P. leucopus* (*P. expansum* Link). He is probably correct.

Penicillium malivorum Cifferi, in Riv. Patol. Veget. **14**: 77–92. 1924. Cifferi's description of his cultures from decaying quinces clearly ally his organism with *P. expansum* Link. His strain was noted as having conidiophores 7.0 to 7.5μ in diameter (hence very large) with smooth walls, but otherwise not differing from many strains seen in culture.

Penicillium plumiferum Demelius, in Verhandl Zool.-Bot. Gesellsch. Wien **72**: 76, fig. 5. (1922) 1923. Demelius described a culture from dried leaves of *Beta vulgaris* var. *ciclae*. She recognized its relationship to *P. expansum* but separated it on account of smaller conidia, greener color, abundance of coremia, and absence of characteristic odor. Conidiophores were described as smooth-walled, up to 2 mm. long by 3.0 to 4.5μ wide, aggregated into plumose coremia, spreading upwards; conidia ellipsoid 2.6 to 3. (3.8)μ by 2.4 to 2.5μ. It seems best to regard the species as a variant of *P. expansum*.

Penicillium variabile Wehmer, in Myc. Centbl. **2**: 195–203. 1913; Compare Ber. Deut. Bot. Gesell. **31**: 210–235. 1913. Wehmer found his organism as a rot of apples and oranges, not found on potatoes, lemons, or onions. A culture received directly from Wehmer was not separable from *Penicillium expansum*. Biourge makes this same observation. There is no ground for maintaining the name.

Penicillium crustosum Thom, in The Penicillia, p. 399. 1930.

Colonies upon Czapek's solution agar attaining a diameter of 4.0 to 4.5 cm. in 10 to 12 days at room temperature, radially furrowed (fig. 131C), in some strains conspicuously so, with central areas often raised and sometimes more or less flocculent, with growing margin about 1 mm. wide, white, otherwise heavily sporing throughout, in yellow-green shades near pea green to sage green (Ridgway, Pl. XLVII), in age becoming brownish approximating cinnamon drab (R., Pl. XLVI), azonate or indistinctly zonate, generally velvety, about 200 to 500μ deep but showing rudimentary fascicles at the growing margin and occasionally larger, scattered fascicles in older colony areas; characteristically developing continuous crusts of conidial chains which break off as irregular masses when the culture dish is struck or tapped (fig. 132); drops inconspicuous, colorless, more abundant in central colony area; odor strong, earthy; reverse colorless or nearly so; penicilli asymmetric, comparatively large, commonly measuring about 40 to 50μ in length, and bearing long tangled chains of conidia up to 150 to 200μ in length; conidiophores comparatively coarse, mostly 200 to 300μ, occasionally up to 500μ in length by 3.5 to 4.5μ wide, conspicuously rough-

ened; penicilli usually consisting of the main axis and one appressed branch 15 to 30μ by 2.5 to 3.5μ, bearing few metulae 10 to 18μ by 2.8 to 3.3μ; sterigmata mostly 8.0 to 10μ by 2.5 to 3.0μ, occasionally 12μ, often borne at different levels in the penicillus; conidia subglobose to slightly elliptical, mostly 3.5 to 4.0μ with walls smooth or nearly so.

FIG. 132. *Penicillium crustosum* Thom on steep agar at two weeks. Culture has been jarred slightly to reveal characteristic crusts of conidia.

Colonies upon steep agar growing somewhat more rapidly, becoming grayish olive (R., Pl. XLVI) within two weeks, shading to light brown in age, generally more closely furrowed and tending to develop heavier conidial crusts but otherwise essentially as described above; odor strong, earthy or moldy; penicilli essentially as on Czapek but bearing spore chains commonly up to 250 to 300μ long, conidiophores more coarsely roughened.

Colonies on malt agar spreading, 6.0 to 6.5 cm. in 12 days, plane, heavy sporing with development of prominent conidial crusts, often zonate (fig. 131D), approximately sage green with green color tending to persist in age;

odor pronounced, moldy; penicilli essentially as the preceding but usually somewhat more compact and borne upon shorter conidiophores, commonly 100 to 150μ in length and very coarsely roughened.

Typical strain produced a limited brown rot (fig. 130D), measuring 1.5 to 2.0 cm. in diameter in 8 to 10 days, when inoculated into sound apples (varieties: Golden Delicious and Winter Banana).

Species description based primarily upon Thom's diagnosis (1930) and upon cultural observations on strains NRRL 968 (Thom's No. 5461.448), received in 1934 from Y. K. Shih, National Wu Han University, Wuchang, China; NRRL 969, isolated as an air contaminant in the Division of Soil Microbiology Laboratory in Washington in 1940; NRRL 943 from C. E. Burnside, isolated from honey bees; and NRRL 1983, received in 1944 from Drs. D. K. Miller and A. C. Rekate, Buffalo, New York as a mold capable of producing an antibiotic that inhibited the growth of the tubercle bacillus. A strain received in February 1946 from the Centraalbureau as Thom's No. 5461.448 remains typical of the species and duplicates NRRL 968 in all essential details. The species was represented in our study by additional strains isolated from chickens in cold storage by Dr. G. A. Ledingham, Ottawa, Canada.

Penicillium flavo-glaucum Biourge (Monogr., La Cellule **33**: fasc. 1, pp. 130–132; Col. Pl. I and Pl. II, fig. 10. 1923) was described in terms which render its separation from *P. crustosum* difficult. Colonies were reported by Biourge (1923) and Thom (1930, p. 386) as zonate, pale to dull green in color with bluish green showing only transiently in marginal areas, and as producing crusts of conidia up to 500μ or more deep, with conidiophores and parts of the penicilli with walls rough. As reported by Thom, and as shown in our current study by a culture received from Biourge in 1924 as type, NRRL 948 (Thom No. 4773.61a), this species differs from *P. cyclopium* primarily in producing colonies less blue-green in color and conidiophores more strongly roughened.

Occurrence and Significance

Members of the *Penicillium expansum* series commonly occur in soil and upon a wide variety of organic substrata. They are, however, best known for their frequent and typical occurrence upon pomaceous fruits, where they produce a destructive rot, commonly referred to as Penicillium-rot, or "blue mold rot," of apples. Brooks, *et. al.* (1920) estimated "blue mold" as the cause of 80 to 95 per cent of the total losses from rot of apples in transit and in commercial storage. Other investigators have published comparable estimates.

Many species and varieties of *Penicillium* occur upon spoiled apples, cherries, grapes, etc., but extensive experiments by ourselves and many others have shown that the members of the *Penicillium expansum* series are by far the most prevalent and the most destructive. In inoculation

experiments, areas of soft brown rot are quickly formed (fig. 130B and C) and rapidly extend to involve the whole fruit (fig. 130A). The development of these areas is usually accompanied by the formation of prominent coremia which subsequently develop powdery masses of blue-green conidia.

The organisms responsible for the decay of apples, grapes, and other non-citrus fruits have been studied by many investigators over a period of many years. Wehmer (1895) discussed, as *Penicillium glaucum*, coremiform structures occurring upon apples and grapes in Hannover. Eustace (1908) studied the apple-rot fungus as it occurred upon fruit in storage in New York. Brooks, *et. al.* (1920), Fisher (1922), and others in the U. S. Department of Agriculture, studied the organisms and devised methods for their control.

Difficulties arising from extended storage and shipment of fruit to Eastern markets and abroad has necessitated thorough investigation of the blue-mold apple rot problem in the Pacific Northwest. Heald and Ruehle (1931) found *Penicillium expansum* capable of rotting apples twice as fast as any other species and reported it to be responsible for 75 per cent of the losses of Washington apples in storage. Heald (1927), Heald and Baker (1932), and Baker and Heald (1932b) discussed methods of controlling blue-mold, with particular reference to the handling, cleaning, and packing of apples. The same authors showed that sodium hypochlorite was very toxic to conidia of *P. expansum*, and later (1934) recommended, as a control measure, that apples be dipped in a rinse containing NaOCl (containing 0.4 per cent available Cl) after the apples had been washed in a HCl cleaner to remove spray residues. Wellman and Heald (1940) investigated the potentialities of many additional chemicals, including several dyes, but made no recommendation for commercial practices. Smock and Watson (1941) and Watson (1943) demonstrated that daily exposures to low concentrations of ozone in storage areas markedly reduced infection and rotting of apples by *P. expansum*.

The mechanism of attack in the destruction of fruit by *Penicillium expansum* has received considerable attention. Nobecourt (1922) attributed the break down of tissue to cytolytic enzymes secreted by the molds, which affords an easy path of entry. Fisher (1922) concluded that *P. expansum* could not penetrate the uninjured surface of the apple but recognized that minute injuries were sufficient to permit invasion. Morse and Lewis (1910), Anderson (1920), and others express similar views, but all agree that sound apples in close contact with rotting fruit can become infected without actual wounding. Kidd and Beaumont (1925) and Baker and Heald (1932a) demonstrated that lenticels provide a common route of entry for *P. expansum* into otherwise sound apples. English, *et al.* (1946) found that washing procedures generally increased the number of

open lenticels and found severe washing to be especially conducive to infection. A period of pre-storage before washing was found beneficial. Kung-Hsiang (1942) demonstrated that the blushed side of apples was less susceptible to infection than the green side; increased resistance was thought to result from the greater amount of pectic substances present in blushed areas. Barnum (1922) suggested that *Penicillium* reached the tissue of the apple only after entering the cut end of the stem and growing through its full length. This has not been confirmed by other workers.

Penicillium expansum occurs less frequently as a cause of rot in other mature fruits. Ciferri in Italy (1924) described *P. malivorum* from quinces in terms which leave no doubt as to its close relationship to *P. expansum*, whatever its minor differences. English (1940) reported it as a cause of decay of pears in Washington. Christoff and Christova (1939) reported *P. expansum* from quinces, pears, and apples in Bulgaria. English and Gerhardt (1942) found *P. expansum* as a cause of decay in sweet (Bing) cherries, and concluded that it could be effectively controlled by exposure to practicable concentrations of CO_2. The same authors (1946) attempted unsuccessfully to control blue-mold on cherries by means of ultra-violet irradiation. Thom (1930) reported *P. expansum* in its coremiform phase to be the usual type of Penicillium-rot occurring upon grapes in storage. Investigations involving similar observations have been made in other countries. Mathieu (1924) reported blue and green Penicillia on grapes in France. Not only was the flavor of the grape pulp affected adversely by the mold, but also that of the must made from the moldy grapes. Aguilera (1926), in Spain, found grapes already packed in barrels to become spoiled by *Penicillium "glaucum"* which attacked the stalks and fruit. *Penicillium* nearly always produced the first signs of rot.

It is safe to assume that *Penicillium expansum* occurs wherever apples and other non-citrus fruits are grown and held in storage, even for limited periods.

Anslow, Raistrick, and Smith (1943) reported the production of the antibiotic patulin by *Penicillium expansum* as well as *P. patulum*, the previously reported source (see p. 537). The antibiotic was found to completely inhibit the growth of various "damping-off" fungi belonging to the genus *Pythium* at concentrations of 1:400- to 500,000, and its possible use in combating such pathogens was discussed. Prior to this, van Luijk (1938) in Holland, had demonstrated the production of substances inhibitory to *Pythium* by unidentified Penicillia isolated from vegetable mold. Apparently these Penicillia found their way into Professor Westerdijk's collection where they were correctly identified, since we received two strains of *P. expansum* marked "v. Luijk α" and "v. Luijk β," respectively, from Baarn in 1946. In all probability van Luijk's inhibitory substance represented

patulin (or whatever name one elects to apply to it—see p. 537). Resuming this work, Duyvene de Wit and others, including van Luyk[1] (1944), described the isolation of a substance, termed "expansine," from *P. expansum* which showed marked inhibitory action against pathogenic bacteria including *Staphylococcus aureus* and *Eberthella typhosa*. Expansine is synonymous with patulin. Kent and Heatley (1945) showed that the substance designated as patulin was largely responsible for the antibiotic activity reported for *P. expansum*, *P. urticae*, and *Aspergillus terreus*.

Miller and Rekate (1944) reported an antibiotic active against *Mycobacterium tuberculosis* to be produced by a *Penicillium* identified by us as *Penicillium crustosum* Thom (p. 518). Yermolieva, *et. al.* (1944) reported a strain of *P. crustosum* to produce an active substance, designated "penicillin-crustosin," which was effective against *Eberthella typhosa* and *Salmonella paratyphi* A and B. The character of the antibiotic remains obscure. A culture received from Yermolieva as *P. crustosum* proved to be a heavy-exudate producing, low-penicillin yielding strain of *P. notatum* Westling.

Since it is a widely distributed and well-known species, *Penicillium expansum* has been studied in a variety of unrelated investigations.

Burgess (1935) reported *Penicillium expansum* to be prevalent upon deteriorating hops, and together with *Aspergillus niger* and *Mucor spinescens* to be responsible for markedly reducing the α-acid in the resins, hence lowering its keeping properties.

Harry (1936) used it as a test organism to evaluate different fungicides for their capacity to prevent mold growth on paint films. Thymol (0.8 per cent) and parachlormetacresol (0.3 per cent) gave the most satisfactory results.

Olson and Macy (1945) used it in evaluating proprionates as inhibitors of mold growth on butter.

Moran, *et al.* (1932) found *Penicillium expansum* to be a common cause of spoilage of meats in cold storage, and used the species as a test organism in evaluating the inhibitory effect of CO_2 on mold growth. Golding (1945) selected *P. expansum*, as one of four common species, for investigating the gas requirements of molds.

Schonwald (1938 and 1941) found spores of *Penicillium expansum* to be abundant in the atmosphere at Seattle, Washington, and demonstrated its role as a causative agent in asthma, hay-fever, and other allergic disturbances.

McCrea (1931) investigating the longevity of molds stored in sealed glass tubes, reported *Penicillium expansum* viable after 8 years.

Manteifel and Shaposhnikoff (1927) reported coremium formation in

[1] Spelled van Luijk in earlier publications.

Penicillium expansum to be enhanced by the accumulation in the substratum of by-products of its metabolism.

McAlister (1938) investigated the effect of the species on the oxidation-reduction potentials of liquid culture media.

Datillo-Rubbo (1938) found a mold resembling *Penicillium expansum* rather than *P. roqueforti* as the dominant species in two Dolce Verdi (a blue-veined type) cheeses.

Skinner (1934), investigated the synthesis of amino acids from $Ca(NO_3)_2$ by a mold reported as *Penicillium flavo-glaucum* (see p. 518). All of the essential amino acids were produced, but with cystine only in small amounts.

Kaess (1934) and Kaess and Schwartz (1935) reported *Penicillium flavo-glaucum* (regarded as *P. crustosum* of this Manual) as responsible for the spoilage of refrigerated meat and investigated the effect of air motion and humidities.

Dox and Neidig (1914) reported the production by *Penicillium expansum* of a new polysaccharide, mycodextran.

"PENICILLIUM GLAUCUM" AND "PENICILLIUM CRUSTACEUM"

Use of the designation *Penicillium glaucum* Link, or simply *P. glaucum*, to cover green, yellow-green, or blue-green Penicillia not otherwise identified, is all too common in the published literature—especially in papers whose content is chiefly biochemical or physiological in character. Link originally (1809) differentiated *P. glaucum* from *P. expansum*, inadequate as the separation was. Later (1924) he grouped the two together and referred to the lot as *P. glaucum*. Today the latter name is practically meaningless and altogether inadequate for reporting work on any specific strain or type of *Penicillium*. *Penicillium crustaceum*, which goes back to Fries (1829) and is today almost equally meaningless, is less commonly but nevertheless often used in the same general and vague sense as *P. glaucum*. A large literature has grown up around both species. In some papers they are referred to along with few to several other molds. These can be ignored for the most part. In other cases whole papers are centered around tests or experiments conducted with a single *Penicillium* referred to as *P. glaucum* or *P. crustaceum*. Sometimes the source of the strain (or strains) gives a clue to its identity, or in other cases some particular reaction may serve to more or less identify the culture studied. Generally, however, there is no way of knowing which of many different green species might have been under observation.

The value of this literature is questionable. However, since we do not wish to ignore it completely, we have included in the Topical Bibliography (Chapter XVI) a number of references to papers centering around these two historic species. Reference to them is introduced at this point in the

text because these names have been used commonly, although by no means consistently, to designate apple rotting Penicillia.

Penicillium italicum Series
(Blue Rot of Citrus Fruits)

Outstanding Characters

Colonies growing rather restrictedly on Czapek but spreading broadly upon steep and malt agars; showing limited to abundant fasciculation of conidiophores, depending upon the strain and the substratum, and usually becoming more prominent with age; conidial areas typically in pale gray-green shades.

Conidiophores arising from the substratum or occasionally from superficial hyphae, commonly aggregated into conspicuous bundles or coremia 1 mm. or more in length and often originating well below the agar surface, smooth-walled.

Penicilli asymmetric, irregularly branched, comparatively long, with metulae and sterigmata often arising at several levels within the penicillus; conidium bearing tips narrowed, often merging almost imperceptibly into the chains of cylindrical to strongly elliptical conidia.

Sclerotia observed in occasional isolates, not in most; regularly disappearing in continued culture.

Odor fragrant, suggesting perfume.

Responsible for the soft "blue-rot" of citrus fruits.

The series is represented by a single, well marked species, *Penicillium italicum* Wehmer. It is rarely found in nature except on citrus fruits where it causes a characteristic soft rot, and where in advanced stages of fruit decay it appears as a bluish green or gray-green mold covering the rind as a velvety or tufted layer of powdery spores. Parallel with the growth of the mold, the tissue of the fruit breaks down largely as a result of the dissolution of the pectic cell wall substance, and a soft and often shapeless mass results. The rot caused by this species is clearly distinct from that caused by *P. digitatum* Saccardo considered earlier (see pp. 385–392). Whereas both types of rot may occur on any of the different kinds of citrus fruits, the *P. italicum* rot appears to be relatively more abundant on oranges and grapefruit and less abundant on lemons than that produced by *P. digitatum*. Both species of *Penicillium* may occur on the same individual fruit.

Wehmer (1895) was the first to distinguish between the two types of citrus rots caused by Penicillia, and named the responsible pathogens *Penicillium italicum* and *P. olivaceum*. He recognized the first as a blue-green species and the latter as an olive-green form. He failed, however,

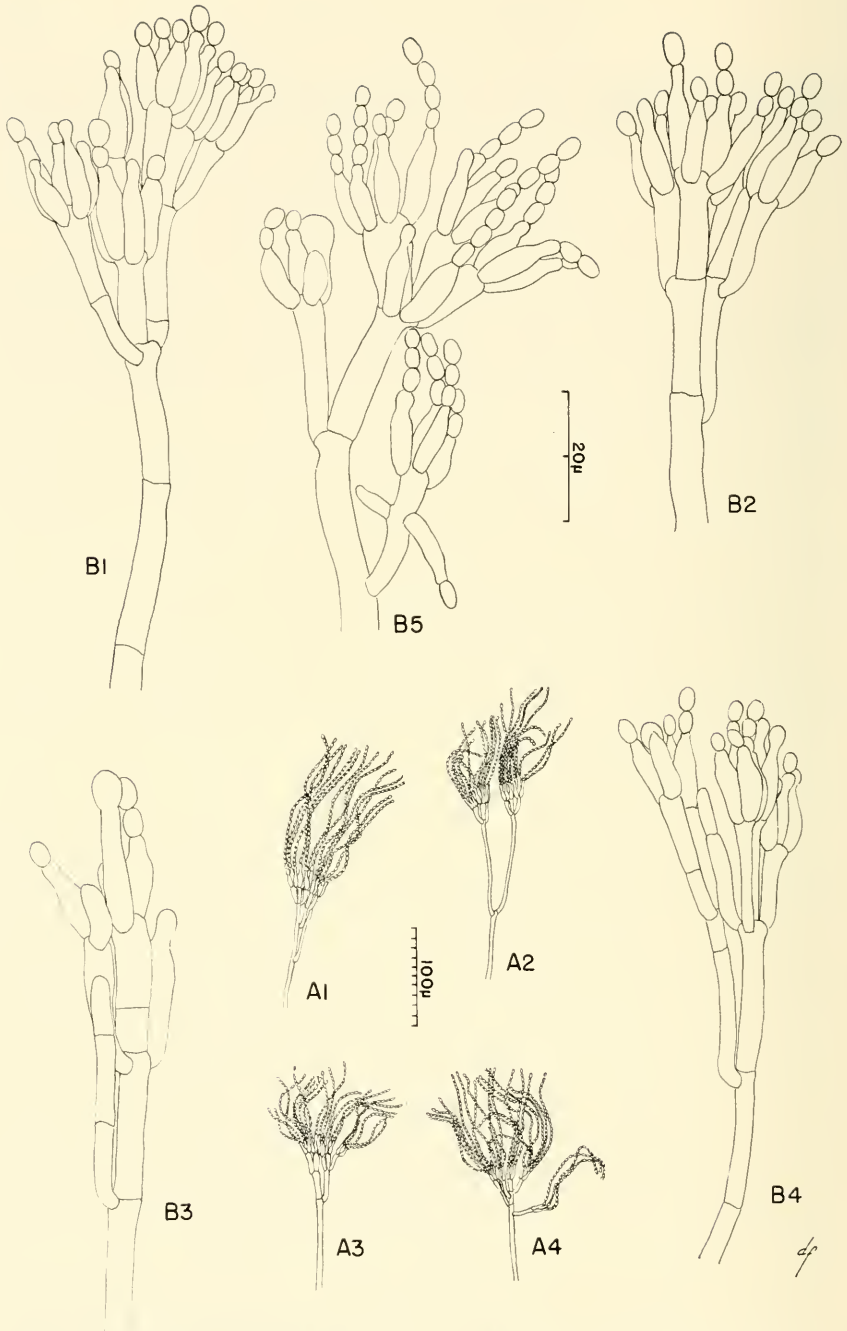


FIG. 133. *Penicillium italicum* Wehmer. A_1–A_4, Habit sketches of representative penicilli showing long divergent and tangled conidial chains. B_1–B_5, Camera lucida drawings showing the variability in over-all pattern and in the arrangement of cellular elements which characterize this species.

to recognize the identity of his *P. olivaceum* with *P. digitatum*, which had been described from oranges and distributed in exsiccati by Saccardo in 1881.

Penicillium italicum normally shows some fasciculation of conidiophores whereas colonies of *P. digitatum*, although loose in texture, remain essentially velvety. *Penicillium italicum* normally produces larger, more complexly branched penicilli in which the constituent elements—*i.e.*, branches, metulae, sterigmata, and conidia—are generally smaller than in *P. digitatum*. *Penicillium italicum*, although somewhat restricted, typically grows more rapidly than *P. digitatum* on Czapek and other synthetic agar

FIG. 134. Lemon infected with *Penicillium italicum* Wehmer showing the type of rot characteristically produced. (Photo by Bureau of Plant Industry, Soils, and Agricultural Engineering, U. S. Department of Agriculture.)

media but not upon such natural substrata as malt extract agar. *Penicillium italicum* produces conidia in pale gray-green or blue-green shades in contrast to the pronounced yellow-green to olive-green conidia of *P. digitatum*. Parallel with these differences, there are certain similarities which should be noted and which may indicate a closer relationship between these species than suggested by their placement in the present Manual. Both species produce very irregular penicilli, particularly *P. digitatum;* both produce strongly elliptical spores, often without showing clear differentiation between the youngest conidia and the tips of the sterigmata; and finally both produce aromatic odors on most substrata.

Doubtfully identified strains can usually be assigned to or separated from the *Penicillium italicum* series by inoculating them into sound citrus fruits (fig. 134). Well-marked areas of rot begin to appear within 2 to 3

days, and within a week usually attain a diameter of 2.5 to 4.0 or 5.0 cm., varying with the strain and the amount of inoculum used. Selected strains almost invariably rot oranges more rapidly than lemons as measured by the diameter of the affected areas. Strains of *P. urticae* Bainier, when similarly inoculated into sound lemons and oranges produce a more restricted, dry, brownish to almost black rot (usually 1.0 to 2.0 cm. in 7 to 8 days) which extends to the center of the fruit, causing a definite purplish discoloration throughout the area of the core. Other species of Penicillium when tested failed to produce any evidence of rot. The limited infections produced by *P. urticae* are regarded as indicating a possible degree of relationship to *P. italicum*, but not sufficiently close to be included in the series with it.

Wehmer described sclerotia in *Penicillium italicum* but failed to find ascospores. Thom (1910) also reported sclerotia but failed to describe them adequately. Schwartz (1926) found a strain of *P. italicum* (identification confirmed by Wehmer) that produced clumps of sclerotia upon oranges, and which, after a twelve-week ripening period, developed ascospores which he reported as smooth-walled, measuring 2.6 by 3.9μ with a narrow equatorial "ring." Although Thom (1930) tried many times, he obtained no ascospores from his transfer of Schwartz's strain. Schwartz's report suggests that he may have been working with some member of the *Carpenteles* series.

Penicillium italicum Wehmer, in Hedwigia **33:** 211–214. 1894. See also Beitr. z. Kennt. Einh. Pilze, II, pp. 68–72; Taf. I, figs. 1–3, Taf. II, figs. 1–10, Jena, 1895. Thom, The Penicillia, pp. 412–414, fig. 63. 1930.

Colonies on Czapek's solution agar growing restrictedly, attaining a diameter of 2.0 to 2.5 cm. in 10 to 12 days at room temperature, with central area 1.0 to 1.5 cm. wide commonly raised and ranging up to 2.0 mm. deep, often marked by a few shallow furrows (fig. 135A), with margins usually thinner and in some strains almost plane but showing evidence of fasciculation, in others strongly fasciculate, sporulating irregularly but seldom heavily, usually more abundantly in marginal to submarginal regions, with conidial areas typically in pale gray-green shades near court gray to gnaphalium green but in some strains more yellowish near pea green (Ridgway, Pl. XLVII); odor fragrant, suggesting perfume, variously diagnosed as "lavender or lilac"; exudate lacking or very limited in amount, clear; reverse variously colored in pale gray to yellowish brown shades, often zonate; conidiophores arising from the substratum or occasionally from superficial hyphae on or near the agar surface, variable in length up to 250μ or more by 3.8 to 5.0μ in diameter, with walls smooth, commonly

developing in conspicuous bundles or coremia up to 1 mm. or more in length, often arising from well below the agar surface, or sometimes, in some strains commonly extending out several millimeters beyond the edge of the colony below the surface of the agar before assuming an erect or ascending position (fig. 135C); penicilli asymmetric, often comparatively long, up to 50 to 70μ bearing tangled chains of conidia (fig. 133A) 100μ or

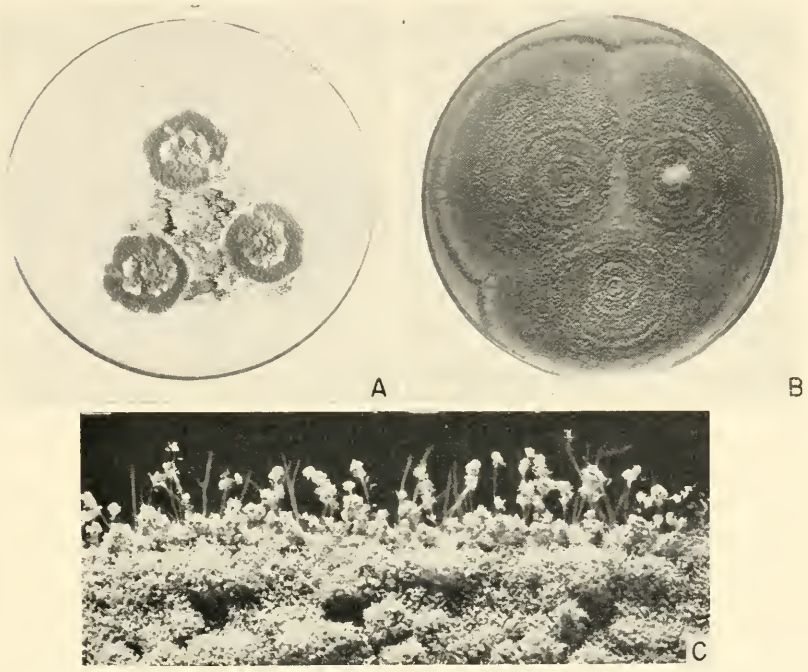


FIG. 135. *Penicillium italicum* Wehmer, NRRL 1293. *A* and *B*, Ten-day old colonies on Czapek and malt agars, showing the restricted development characteristic of the former and the broadly spreading colonies typical of the latter. *C*, Margin of three-week old colony on Czapek agar showing characteristic coremia emerging from the substratum and other bundles of hyphae that are still wholly submerged, × 10.

more in length, usually consisting of the main axis and 1 to 3 branches variously produced at the upper nodes of the stalk, commonly measuring 15 to 25μ by 2.8 to 4.4μ but occasionally much longer and often rebranched; metulae born singly or in groups of 2 to 4 (fig. 133B), measuring 15 to 20μ by 3.5 to 4.0μ but frequently larger or smaller, normally arising at different levels in the penicillus; sterigmata relatively few in number, mostly in clusters of 3 to 6, extremely variable in dimensions, commonly 8 to 12μ by about 3.0μ but ranging from 2.0 to 5.0μ in diameter and not infrequently 15μ long, with apices often merging almost imperceptibly into the chains

of conidia; conidia at first typically cylindrical but becoming definitely elliptical or even subglobose at maturity (fig. 133B), dimensions extremely variable but generally 4.0 to 5.0μ by 2.5 to 3.5μ, with individual spores when elliptical ranging up to 9.0 by 5.0μ or 6.6μ when subglobose, walls smooth, appearing pale yellow-green in mass.

Colonies on steep agar spreading broadly, attaining a diameter of 5.0 to 6.0 cm. in 10 to 12 days at room temperature, plane except for shallow radial furrows, heavily sporing, generally in glaucous gray shades (R., Pl. XLVIII), with surface usually appearing granular or tufted throughout and with marginal areas commonly showing prominent fasciculation; odor less pronounced but essentially as on Czapek; no exudate produced; reverse at first in dull yellowish shades but soon darkening, and in mature colonies often showing dark to blackish coloration in radiating lines or sectors; penicilli essentially as described above but commonly larger than on Czapek.

Colonies on malt extract spreading broadly, 5 to 6 cm. in 10 to 12 days at room temperature, typically plane, heavily sporing (fig. 135B), with entire colony often appearing coarsely granular from the abundant development of clustered conidiophores; odor as described above but often less marked; no exudate; reverse in dull yellow-brown shades with blackish sector-like areas often conspicuous; penicilli comparatively "stocky" and showing great variation in the dimensions of parts but generally exhibiting the pattern described on Czapek; conidia show great variation in size and shape, with individual cells commonly up to 7.0μ or more in long axis.

Individual strains may vary appreciably in the degree of fasciculation shown and in their general rate of growth. Some grow rapidly and fill the entire agar plate or tube, others are more restricted and seldom exceed 3.0 to 4.0 cm. in diameter on Czapek agar even after three or four weeks. All grow more luxuriantly upon malt extract and steep agars; and on Czapek there is some evidence that many strains suffer from a limited nutrient deficiency. Particular isolates often show considerable intrastrain variation, and it is commonly possible to isolate from a single culture different substrains which show marked variation in rate of growth, amount of sporulation, general colony texture and color, and in the abundance and size of fascicles or coremia produced. It thus becomes somewhat difficult to describe the species in tangible terms and yet make such a diagnosis sufficiently general to embrace all of the strains belonging in it.

Cultures long maintained upon laboratory media commonly show progressively lighter sporulation, which may be accompanied by a decreased pathogenicity. Members of this series are comparatively short-lived, and cultures should be re-transferred at comparatively frequent intervals to insure viability. New isolates, however, can almost always be secured at the nearest fresh fruit market and stocks can be easily replenished.

For routine laboratory studies it is actually better to obtain such fresh cultures, for they are generally most characteristic of the species.

Species description based upon the examination of numerous strains some of which are contained in the permanent collections of the Northern Regional Research Laboratory, and a limited number of which represent recent isolates from freshly spoiled citrus fruit. The following cultures may be regarded as representative: NRRL 983, from Dr. H. S. Fawcett, Citrus Experiment Station, Riverside, California, in 1930; NRRL 1293, isolated from a rotting orange, at the Northern Regional Research Laboratory, Peoria, Illinois, in 1941; and NRRL 1900, from Professor Gladys E. Baker, Vassar College, Poughkeepsie, New York, in 1943. This list could be extended, but to little advantage.

Two additional species were included in the *Penicillium italicum* series by Thom in 1930, namely: *P. aeruginosum* Dierckx and *P. ventruosum* Westling. The validity of both usages was questioned at that time and the subsequent examination and comparison of many additional cultures substantiates this belief.

Penicillium aeruginosum Dierckx (Soc. Scient. Brux. **25**: 87. 1901). Dierckx himself regarded his species as possibly representing *P. olivaceum* of Wehmer, but in later unpublished notes (*fide* Biourge, 1923, p. 121) he concluded that it represented Wehmer's *P. italicum*, an opinion with which we heartily agree. Biourge in his Monograph (1923, pp. 121–123, Col. Pl. I, fig. 6) re-established the species to cover a strain in his possession which produced prominent coremia and which apparently failed to produce sclerotia as observed by Wehmer (1894) and Thom (1910). Variation within the *P. italicum* series is great, particularly with regard to the production of prominent fascicles or even coremia; while we recognize that strains such as Biourge's do occur, we cannot believe that they merit recognition as a separate species.

Penicillium ventruosum Westling (Arkiv för Botanik **11**: 57, 112–114; figs. 26 and 67. 1911). This species has commonly been interpreted as including members of the *P. italicum* series that produce conspicuous coremia, which, in marginal colony areas, are often prostrate and may extend for several millimeters beneath the agar surface before emerging to produce conidia. Except for this habit, there is little to separate such forms from the more typical strains which are normally regarded as representing *P. italicum* Wehmer. The separation might be regarded as valid were it not for the fact that strains varying greatly in their tendency to produce coremia can be isolated from miscellaneous collections of rotting citrus fruits, and for the additional fact that the structural details of the penicilli and the measurements of parts including conidia are essentially the same whether or not prominent coremia are produced. Westling suggested the possible relationship of his species to *P. italicum*, and it is our belief that it should be regarded as synonymous with this generally accepted species.

Occurrence and Significance

Although it is occasionally isolated from soil and other substrata, *Penicillium italicum* Wehmer typically occurs on citrus fruits where it produces

a characteristic soft rot, generally referred to as "blue-mold rot." Together with *P. digitatum* Sacc., it is responsible for serious losses of oranges, lemons, grapefruit, etc., particularly during storage and marketing. The two species may occur separately or together, but in either case, problems relating to infection and control are common to both species, hence a joint literature has been built up. (See also the *P. digitatum* series, p. 385 to p. 392.)

Penicillium italicum as a cause of decay of citrus fruits in this country has received careful study by Fulton, Brooks, Miller, and others in the U. S. Department of Agriculture, by investigators in Florida, and by Fawcett and co-workers in California.

Barker (1928) reported *Penicillium digitatum* and *P. italicum* commonly developing on citrus fruit arriving in London from Spain, Palestine, Brazil, and Argentina. Powell (1928), and Reichert and Littauer (1928) found *P. italicum* and *P. digitatum* prevalent on fruits in Palestine and recommended careful handling, sanitation, and disinfection of fruit with hypochlorite, sodium bicarbonate, or borax as measures of control. Tindale and Fish (1931) reported the same mold to be responsible for heavy infections in Victoria; and as a control measure, they recommended storing fruit for 3 days at 94°F. prior to placement in storage. Kursanoff and Alexeyeva (1938) observed heavy losses from blue and green mold citrus rots in Southern Russia. Wei (1940) found *P. italicum* to be the most destructive rot of sweet oranges in Szechuan Province, China. A new variety, *P. italicum* var. *album* Wei, characterized by white colonies, and *P. fructigenum* Takeuchi were reported. Benton (1931) reported Penicillium rots to be common on oranges in New South Wales, Australia, and recommended dipping the fruit in 8 per cent borax solution and covering with paraffin before storing. Nattrass (1935) reported *P. italicum* and *P. digitatum* to be common on fruit in Cyprus. Kidd and Tompkins (1928) studied temperature in relation to spoilage of South African Valencia oranges, reporting *P. italicum* to be the most destructive species in storage at 5°C.

Fawcett (1927) found *Penicillium italicum* to be the most common cause of contact rot in stored lemons, with the mold spreading from diseased to sound fruit. Savastano and Fawcett (1929) studied the effect of mixed inocula in producing decay of wounded orange and lemon fruits, and in some cases found the rate of spoilage to exceed the sum of the rates of individual pathogens. Barger (1928) showed that sodium bicarbonate could be substituted for borax as a disinfectant to protect fruit against *P. digitatum* and *P. italicum*. Marloth (1931) investigated the influence of H-ion concentration and of sodium bicarbonate upon the growth of *P. italicum* and *P. digitatum* upon synthetic media with added orange extract. The

favorable growth range of the former was pH 2.9 to 6.5, for the latter 3.0 to 6.0. The bicarbonate-ion (pH 8.4 in solution) was regarded as toxic to these fungi and its fruit-protective action was attributed to the thin film of the salt which remained after the fruit was dipped. Tompkins (1930) studied the effect of acetaldehyde upon the growth of different citrus pathogens, including *P. italicum* and *P. digitatum*. Germination of conidia was inhibited or delayed at concentrations of 2 to 5 in 10,000, whereas much higher concentrations were necessary to kill. Lowering the temperature markedly reduced its effectiveness. Melkon (1938) found iodide, bromide, and chloride of lithium to be decreasingly toxic to *P. italicum*. Klotz (1934, 1936) studied the effectiveness of nitrogen trichloride and other gases in controlling decay in oranges, reporting concentrations of NCl_3 as low as 4–6 mg./cu. ft. to be lethal to conidia of *P. italicum*, *P. digitatum*, and other fungi after 30 minutes exposure. Chlorine was more injurious to the fruit and afforded less protection. NHMeCl could be substituted for NCl_3 but was more costly. Ozone showed only limited toxicity to the Penicillia and gave no protective action to the fruit. Sulphur dioxide could be used effectively for sterilization of boxes and equipment. Robson (1935) confirmed Klotz's observations regarding the effectiveness of NCl_3 as a gaseous fungicide.

Gioelli (1932) observed some degree of "antagonism" between *Penicillium italicum* and *P. digitatum* when both occurred upon the same fruit, the latter commonly surrounding but not invading areas infected by the former species. Controlled laboratory experiments were subsequently made using whole fruit, orange and lemon rind, and synthetic media. Thermostable toxins capable of ultra-filtration were isolated from both molds.

Little biochemical work with *Penicillium italicum* has been reported. Oxford and Raistrick (1932) reported the isolation of ergosteryl palmitate from *P. italicum* and strains of *P. brevi-compactum* Dierckx (see p. 417). Birkinshaw, Charles, and Raistrick (1931) isolated from different strains of *P. italicum* a substance giving an emerald-green color with $FeCl_2$ and a purple color with bleaching powder solution. The authors regarded these color reactions as of diagnostic value since they were not observed in other species investigated.

Karrer (1921) studied the influence of H-ion concentration upon amylase production by *Penicillium italicum*.

Penicillium urticae Series

Outstanding Characters

Colonies growing rather restrictedly, with margins abrupt, comparatively deep from 1.0 to 2.0 mm. or more, with surface distinctly granular and

with prominent fascicles typically produced in marginal areas, heavily sporing throughout, in light gray-green shades.
Conidiophores simple or in fascicles, undulate or sinuate, smooth-walled, up to 400 to 500μ or more in length.
Penicilli asymmetric, variable in pattern, loosely divergent, often twice-branched below the level of the metulae, with metulae comparatively short and sterigmata unusually small and numerous in the verticil.
Conidia thin-walled, smooth, elliptical to subglobose.
Cultures usually producing a distinctive fragrant odor.

The series is represented by a single variable species to which either of two names might be properly applied, namely: *Penicillium patulum* Bainier and *P. urticae* Bainier. The first of these species was inadequately described, but fairly accurately illustrated in 1906. The second species was described a year later in more detailed and precise terms, but obviously approximated *P. patulum.* Cultures believed to represent types of both species have been preserved and were included in the present study. No significant differences were observed. Since Bainier's description of *P. urticae* is more accurately drawn, we prefer to recognize this rather than the older name *P. patulum.* The general series is referred to under the same designation.

Members of the series are easily recognized by the characters listed above. Especially diagnostic are the rather restricted, granular to fasciculate colonies in gray-green to pale yellow-green shades; the loose rangy character of the penicilli; and the crowded verticils of unusually small sterigmata (fig. 136B).

When inoculated into sound citrus fruits, members of the series produce black to dark brown necrotic areas 1.0 to 1.5 cm. in about 10 days, and throughout the central area produce a pronounced purplish coloration, but without marked evidence of tissue destruction. They can hardly be regarded as parasitic. They are occasionally isolated from citrus or other types of fruit, but typically appear to represent decay organisms that may be expected to appear upon a variety of decomposing vegetable material.

All members of the series, apparently, produce an antibiotic, reported in 1943 by Professor Raistrick and co-workers as "patulin," but later shown to be identical with claviformin, clavacin, etc. (see p. 537).

Thom, in 1930, drew a distinction between *Penicillium urticae* Bainier and *P. patulum* Bainier upon the basis of culture odors: *Penicillium urticae* being reported as characterized by the production of a peculiar and distinctive ethereal odor, whereas *P. patulum* produced little or no odor. Careful examination of many cultures with regard to this character has

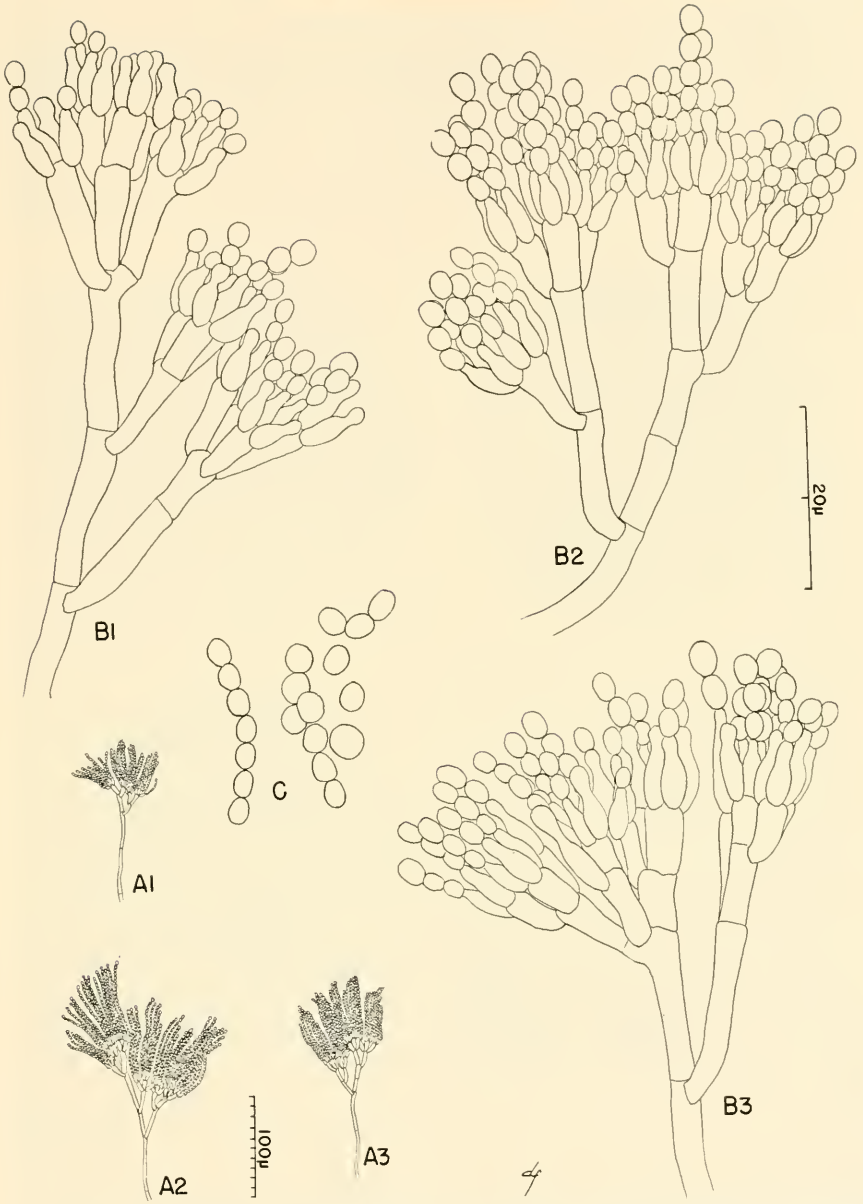


FIG. 136. *Penicillium urticae* Bainier. A_1–A_3, Habit sketches of large, rebranched penicilli representative of the species. B_1–B_3, Camera lucida drawings of typical penicilli—note particularly the short sterigmata which characterize this species.

failed to establish any reliable point of separation and we no longer believe it possesses diagnostic significance.

Penicillium urticae Bainier, in Bul. Soc. Mycol. France **23:** 15–16, Pl. IV, figs. 1–5. 1906; ibid. **23:** Pl. V, figs. 10–16. 1907. Thom, The Penicillia, pp. 418–419. 1930.

Synonyms: *P. patulum* Bainier, in Bul. Soc. Mycol. France **22:** 208, Pl. XI, figs. 14–17. 1906.

P. flexuosum Dale, in Ann. Mycol. **24:** 137. 1926, previously published in Biourge's Monogr., La Cellule **33:** fasc. 1, pp. 264–265; Pl. XIX, fig. 110. 1923.

Colonies on Czapek's solution agar growing restrictedly, attaining a diameter of 2.0 to 2.5 cm. in 12 to 14 days at room temperature, radiately furrowed in most strains (fig. 137A), with margins abrupt and with central area often somewhat raised, ranging from 0.5 to 1.0 mm. deep in marginal areas to 2.0 to 3.0 mm. deep in colony centers; surface distinctly granular in most strains, with prominent fascicles usually produced at least in the marginal areas, heavily sporing throughout, approximately gnaphalium green (Ridgway, Pl. XLVII), in some strains less heavily sporing and somewhat floccose, approximately court gray (R., Pl. XLVII), and in occasional heavily sporing strains appearing darker green near pea green or artemisia green (R., Pl. XLVII); exudate not produced in some strains, abundantly in others with droplets typically large, clear or nearly so, and often largely embedded in the colony mass; odor distinctive and fragrant in some strains, not pronounced in others; reverse at first dull yellow becoming orange cinnamon (R., Pl. XXIX) to reddish brown shades, with agar slightly colored beyond the colony margin; penicilli loosely divergent, comparatively large but extremely variable in pattern and dimensions, commonly 40 to 50μ in length but ranging from 20 to 80μ, bearing more or less divergent conidial chains up to 50 to 100μ in length (fig. 136A); conidiophores partly in fascicles, partly simple, undulate or sinuate (fig. 136A_3), with walls smooth, commonly ranging up to 400 to 500μ or more in length by 3.0 to 4.0μ in diameter; penicilli variously branched with conidium bearing elements commonly arising at different levels (fig. 136B); branches divergent but mostly 15 to 20μ by 3.0 to 3.5μ ranging from 12 to 30μ by 2.8 to 4.0μ; secondary branches, when present, mostly 12 to 15μ by 3.0 to 3.5μ, but ranging from 10 to 20μ by 2.5 to 3.5μ; metulae comparatively short, mostly 7 to 9μ by 3.0 to 3.5μ, commonly in groups of 2 to 4; sterigmata short, 4.5 to 6.5μ by 2.2 to 2.5μ, crowded in the verticil (fig. 136B), commonly in clusters of 8 to 10; conidia elliptical or tardily subglobose (fig. 136C) mostly 2.5 to 3.0μ in long axis with walls thin, smooth.

Colonies on steep agar growing somewhat more rapidly, 3.0 to 3.5 cm. in 12 to 14 days, in appearance and texture essentially as on Czapek (fig. 137B) but generally heavier sporing, and with greater exudate production; odor not characteristic; reverse in dull brown shades; penicilli as on Czapek.

Colonies on malt agar 2.5 to 3.0 cm. in 12 to 14 days, generally plane (fig. 137C) with surface appearing granular and with marginal areas more or less zonate; in some strains strongly fasciculate throughout, in others with prominent fascicles produced abundantly only in the marginal areas, and in occasional strains more or less floccose and showing only reduced fasciculation; penicilli essentially as on Czapek but generally more compact.

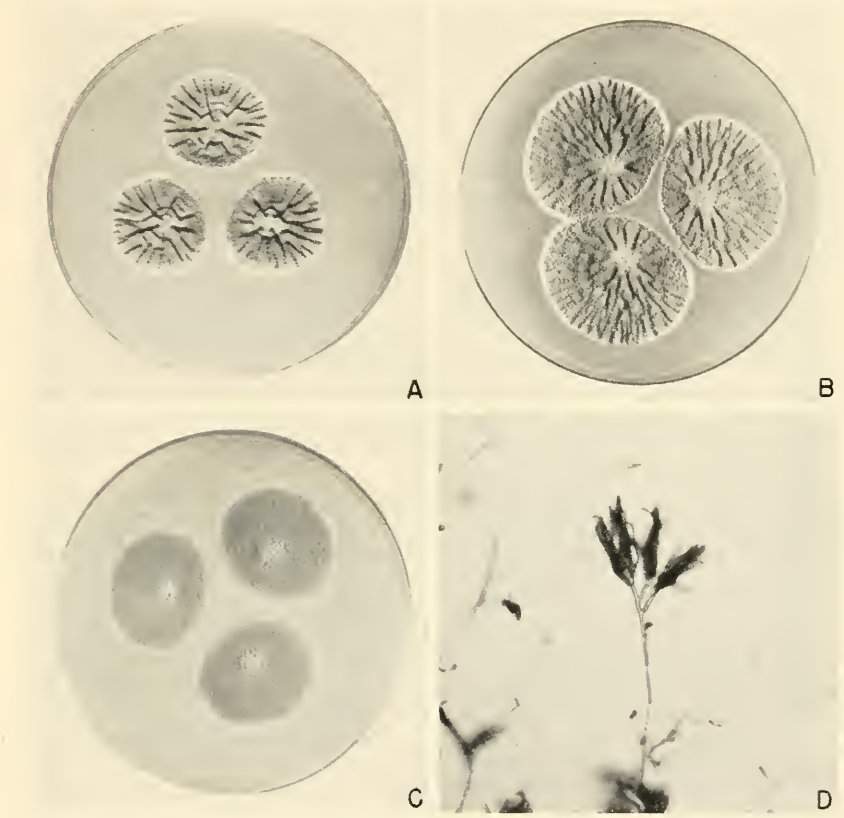


FIG. 137. *Penicillium urticae* Bainier, NRRL 989. *A*, *B*, and *C*, Ten-day old colonies on Czapek, steep, and malt agars, respectively. *D*, Single penicillus as seen under 8 mm. objective, × 110.

Species description based upon comparative cultural and microscopical examination of many strains received or diagnosed as *Penicillium urticae* Bainier, *P. flexuosum* Dale, or *P. patulum* Bainier. The following cultures contained in the NRRL Collection may be regarded as representative: NRRL 989, received from the Thom Collection as No. 4640.455, as Bainier's type of *P. urticae;* NRRL 994, from the Thom Collection as No.

4640.454, originally from da Fonseca and believed to represent Bainier's type of *P. patulum;* NRRL 992 from the Thom Collection as No. 2694, representing the type of *P. flexuosum* Dale and regarded by Thom (1930, p. 419) as representing *P. urticae;* NRRL 991, received from Dr. Julian Cohn, Los Angeles, California, in 1936 and diagnosed as *P. urticae;* NRRL 1952 and 1953, received from Professor Raistrick as the strains of *P. patulum* (LSHTM Catalogue No. P. 189 and Ad. 77, respectively) employed to produce patulin in their study of this antibiotic (1943); and a strain received from the Centraalbureau in May 1946 as *P. urticae*, originally from Dale in 1914, hence presumptively identical with NRRL 992.

White mutant: A mutant characterized by white colonies and abundant white conidia was isolated in October 1946 from a sector variant in a typical culture of *Penicillium urticae* received from Dr. John Ehrlich as a patulin producer. Except for an absence of green color the mutant appeared to duplicate the parent strain (Col. Pl. I).

Penicillium griseo-fulvum Dierckx (Soc. Scien. Brux. **25:** 88. 1901) was discussed by Biourge (Monogr., La Cellule **33:** fasc. 1, pp. 164–167; Col. Pl. II and Pl. II, fig. 11. 1923) as a somewhat floccose form with large, loose coremia 4 to 12 by 2.5 mm., with stalks white or yellowish and reverse yellow to fulvous. Conidiophores were smooth-walled and about 5.0μ in diameter. Penicilli were comparatively large and irregularly branched, sometimes producing metulae and sterigmata at the same level. Sterigmata were recorded as 7 to 8 or even 11 by 3.5 to 4.0μ. Conidia were globose, mostly 2.5 to 3.5μ but up to 5.0μ in diameter.

Thom (1930, p. 371), reported Biourge's culture No. 34, received under the above name and possibly type, to produce loosely massed aggregations or almost coremiform tufts in predominantly floccose colonies 2 to 3 mm. deep. No detailed measurements of penicilli were given. The culture studied by Thom was subsequently lost from our Collection. However, two cultures apparently duplicating the above were included in the present study. One of these was received from the Centraalbureau in March 1946 as *P. griseo-fulvum* Dierckx from Biourge in 1927. The second culture was received from George Smith, London School of Hygiene and Tropical Medicine as "P-68 (= Biourge's No. 34)". Both of these cultures grow restrictedly and sporulate very lightly upon Czapek and steep agars, and both show a marked tendency to develop fascicles when grown on malt extract agar. The culture from Smith is heavier sporing and on malt agar produces large, rebranched penicilli that are entirely characteristic of the *P. urticae* series. The one from Baarn produces scattered and generally smaller structures of similar pattern.

The correct assignment of *Penicillium griseo-fulvum* Dierckx remains in doubt. Thom, in 1930, placed it in his Asymmetrica-Funiculosa with *P. terrestre* Jensen, and the measurements of metulae and sterigmata given by Dierckx (1901) and Biourge (1923) might support such placement. If, however, we base assignment upon the cultures now in our possession, and which we have reason to believe represent the one studied by Biourge, then the species should be placed in the series with *P. urticae* Bainier. Sterigmata are quite small, measuring about 5.0 to 6.0μ in length, conidial areas are pale green near mineral gray to gnaphalium green (Ridgway, Pl. XLVII) and colonies are deep reddish brown in reverse. All of these characters typify the

P. urticae series. Furthermore, the culture closely resembles this series in its biochemical behavior (see below).

Occurrence and Significance

Penicillium urticae Bainier appears to be widely distributed but not particularly abundant in nature. Its typical habitat is soil, but cultures have been isolated from decaying vegetation, sheep dung, and other substrata. Their role in decomposition processes has not been investigated.

Biochemically, principal interest in the series centers around the production of an antibiotic reported by Raistrick, *et al.* (1943) and Anslow, Raistrick, and Smith (1943) to be produced by strains of *Penicillium patulum*, hence designated patulin. The same antibiotic has been reported from other species of *Penicillium* and *Aspergillus* under different names by other investigators. Upon a basis of priority two of these, claviformin and clavacin, take precedence over the name patulin. Largely because patulin was first announced as possessing curative value for treatment of the common cold (Raistrick, *et al.*, 1943), the name received immediate and wide acceptance. This name is probably still used more commonly than any other, although claviformin is probably the name which should be recognized. The history of this antibiotic, which is of considerable interest, has been summarized by Lochhead, Chase, and Landerkin (1946) as follows:

"In 1942 Wiesner reported the concentration of a substance from culture filtrates of *Aspergillus clavatus* that inhibited growth of *Staphylococcus aureus*. Waksman, Horning, and Spencer (1942) likewise found the same fungus to yield an antibiotic substance, obtained as a crude concentrate, that was active against a variety of Gram-negative, as well as Gram-positive, bacteria and that was named clavacin. At the same time Chain, Florey, and Jennings (1942) isolated from culture filtrates of *Penicillium claviforme* a crystalline compound, active against Gram-negative and Gram-positive organisms, to which the name claviformin was given. In 1943 Anslow, Raistrick, and Smith and Raistrick *et al.* (1943) reported the isolation of patulin, an antibiotic substance produced by *Penicillium patulum* and *P. expansum*, obtainable in crystalline form, with the empirical formula $C_7H_6O_4$, and for which the structure anhydro-3-hydroxymethylene-tetrahydro-γ-pyrone-2-carboxylic acid was proposed.

"From the metabolism solution of Wiesner's strain of *A. clavatus*, Bergel *et al.* (1943) isolated, as a crystalline entity, an active substance to which the name clavatin was applied and that was found identical with claviformin. Furthermore, Bergel *et al.* (1944) established the identity of clavatin with patulin, which latter was shown by Chain *et al.* (1944) to be similar to claviformin. In the meantime Hooper *et al.* (1944) reported clavacin to be identical with patulin, a finding confirmed by Katzman *et al.* (1944). It appears, therefore, that claviformin, clavacin, clavatin, and patulin are the same substance. Since claviformin appears to have been the term first used for the crystalline material this name is used in this report."[2]

[2] Dates substituted for numbered references cited in Lochhead, Chase, and Landerkin.

As noted earlier (see p. 520), the antibiotic under consideration is also produced by *Penicillium expansum* Link (Anslow, Raistrick, and Smith, 1943), and material of this origin has been referred to as expansine by Duyvene de Wit, *et al.* (1944). Karow and Foster (1944) found it to be produced also by a species of *Gymnoascus* and two unidentified Penicillia. Kent and Heatley (1945) obtained it from a culture identified as *P. urticae* Bainier, with which *P. patulum* is synonymous. Atkinson (1942, 1943) reported an antibiotic, designated penicidin, from a culture approximating *P. terrestre* Jensen which is believed to be identical with claviformin. The production of this antibiotic is not restricted to the genus *Penicillium*, but within the genus it does seem to be more or less characteristic of certain species of the Fasciculata and forms possibly closely related.

Unfortunately, subsequent investigators failed to substantiate the original claims for patulin (claviformin) as a cure for the common cold (Stansfeld, Francis, and Stuart-Harris, 1944). Furthermore, it is now generally agreed (Broom, *et al.*, 1944) that the antibiotic is too toxic to permit therapeutic use that involves injection into animals or man. Herrick (1945) and Sanders (1946) have shown that it is highly fungistatic, hence may find application in the treatment of superficial fungus infections in man and animals. Laboratory experiments reported by Anslow, Raistrick, and Smith (1943), and Timonin (1946) suggest its possible use in combating certain plant-disease-producing fungi.

Professor Raistrick and his associates have published a series of papers on the biochemistry of a culture received from Biourge, as *Penicillium griseo-fulvum* Dierckx (Biourge's No. 34). For reasons noted above, we believe this culture represents a member of the *P. urticae* series. Anslow and Raistrick (1931) isolated 6-hydroxy-2-methylbenzoic acid (6-methylsalicylic acid) as a product of the metabolism of glucose (yield 2.42 per cent). The compound crystallized from chloroform as white needles and melted without decomposition at 170–171°C. It had the empirical formula $C_8H_8O_3$ and was believed to be phenolic in nature since it gave a purple color with $FeCl_3$.

A second metabolic product, gentisic acid (2:5-dihydroxybenzoic acid) was isolated by Raistrick and Simonart (1933) from cultures of *Penicillium griseo-fulvum* grown upon a Czapek-Dox medium containing 8 per cent glucose and 0.25 per cent $NaNO_3$. Mannitol and fumaric acid were also isolated.

Griseofulvin, $C_{17}H_{17}O_8Cl$, still another metabolic product, was isolated by Oxford, Raistrick, and Simonart (1939) from cultures grown upon media containing glucose as the sole source of C.

Simonart (1934) studied the influence of temperature on the production of 6-methylsalicylic and gentisic acids by *Penicillium griseo-fulvum* but observed no marked difference between 24° and 30°C.

Birkinshaw, Bracken, and Raistrick in 1943 reported the isolation in fair yield of gentisyl alcohol (2:5-dihydroxybenzyl alcohol), along with the antibiotic patulin, from the culture filtrate of *Penicillium patulum* grown upon Raulin-Thom medium. The product was obtained as a colorless crystalline sublimate, M.P. 100°C, having the empirical formula $C_7H_8O_3$. Gentisic aldehyde and gentisic acid were also identified as metabolic products of *P. patulum*.

As noted earlier (see p. 154), Oxford, Raistrick, and Simonart (1935) reported fulvic acid, a yellow crystalline pigment, as a metabolic product of *Penicillium griseo-fulvum* Dierckx, *P. flexuosum* Dale, and *P. brefeldianum* Dodge.

The production of the same metabolic products cannot be taken *per se* as evidence of the identity, or close natural relationship of two different cultures of Penicillia. Oftentimes, however, such production is indicative of a natural relationship. We believe this to be true in the case of Biourge's so-called *Penicillium griseo-fulvum* Dierckx, strain No. 34. Cultural and morphological criteria indicate a close similarity between this strain and *P. urticae* Bainier. The production of gentisic acid by this strain and of gentisic acid and gentisyl alcohol by *P. patulum* (= *P. urticae*) affords additional evidence of relationship. Finally, the production of fulvic acid by this strain and by *P. flexuosum* (= *P. urticae*) is believed to furnish still further evidence of such relationship. The production of fulvic acid by *P. brefeldianum*, on the other hand, represents a case where biochemical behavior appears to be independent of natural relationships, since the two species are strikingly different in both cultural and morphological characteristics.

Penicillium granulatum Series

Outstanding Characters

Colonies are typically strongly fasciculate with a majority of the conidiophores aggregated into well-marked fascicles or coremia up to 2 mm. or more high, but with simple conidiophores regularly produced and in older stock cultures often predominating. Conidiophores comprising the coremium tending to diverge and often terminating as a feathery mass of conidial structures.

Conidiophores variable in length depending upon the strain and the substratum, arising primarily from submerged hyphae, with walls conspicuously roughened and with branches and metulae usually similarly but less prominently marked.

Penicilli large, asymmetric, usually showing one or more branches in addition to the main axis and with each major element bearing successively verticils of metulae and sterigmata with conidia in tangled chains.

Series Key

1. Fascicles or coremia predominating but interspersed with abundant simple conidiophores; conidiophore walls roughened..... *P. granulatum* series
   a. Conidia globose to subglobose; colonies 1.0–2.0 mm. deep; conidial areas in yellow-green to dark yellow-green shades; odor usually not pronounced. *P. corymbiferum* Westling
   b. Conidia elliptical; colonies 2.0–4.0 mm. deep; in pale blue-green to glaucous shades; odor pronounced, aromatic..... *P. granulatum* Bainier

Two fairly well differentiated species comprise the series, namely: *Penicillium corymbiferum* Westling and *P. granulatum* Bainier. Both species are characterized by the production of abundant and conspicuous fascicles or loosely constructed coremia that are more highly developed than those of the several series previously considered but less so than those of the *P. claviforme* series which follows. Penicilli are quite large, usually branched, and are consistently borne upon conidiophores with conspicuously roughened walls. The series seems to grade almost imperceptibly into the *P. expansum* series, for individual isolates which appear transitional between the two series are not infrequently encountered. Such intermediate forms, however, rot apples very slowly if at all, hence appear to be characterized by physiological differences which separate them from the *P. expansum* series.

Members of the series may be regarded primarily as soil forms and appear to be fairly widely distributed in nature. *Penicillium corymbiferum* commonly occurs upon liliaceous bulbs and root stocks and under certain conditions may become pathogenic.

Freshly isolated strains usually present a strongly fasciculate appearance which represents the typical cultural aspect of the series, whereas strains long maintained in laboratory culture often tend to lose this character and to become either increasingly floccose or almost velvety.

Penicillium corymbiferum Westling, in Arkiv för Botanik **11**: 56, 92–95; figs. 16, 58. 1911. Thom, The Penicillia, pp. 423–425. 1930.

Colonies on Czapek's solution agar (Col. Pl. VIII) growing rapidly, attaining a diameter of 4.5 to 5.0 cm. in 8 to 10 days, up to 1.0 to 2.0 mm. deep in central to subcentral areas, azonate or indistinctly zonate near colony margins, strongly fasciculate (fig. 139A), with surface appearing coarsely granular or ridged and with the majority of conidiophores aggregated into clearly defined bundles easily viewed at the colony margin (fig. 139C) or in radial colony sections, heavily sporing throughout, with growing margin and secondary tufts of vegetative hyphae and developing conidiophores white to pale yellow, passing through yellow-green shades near pea green to sage green (Ridgway, Pl. XLVII) with the development of mature conidia, and becoming slate-olive (R., Pl. XLVII) in age; exudate

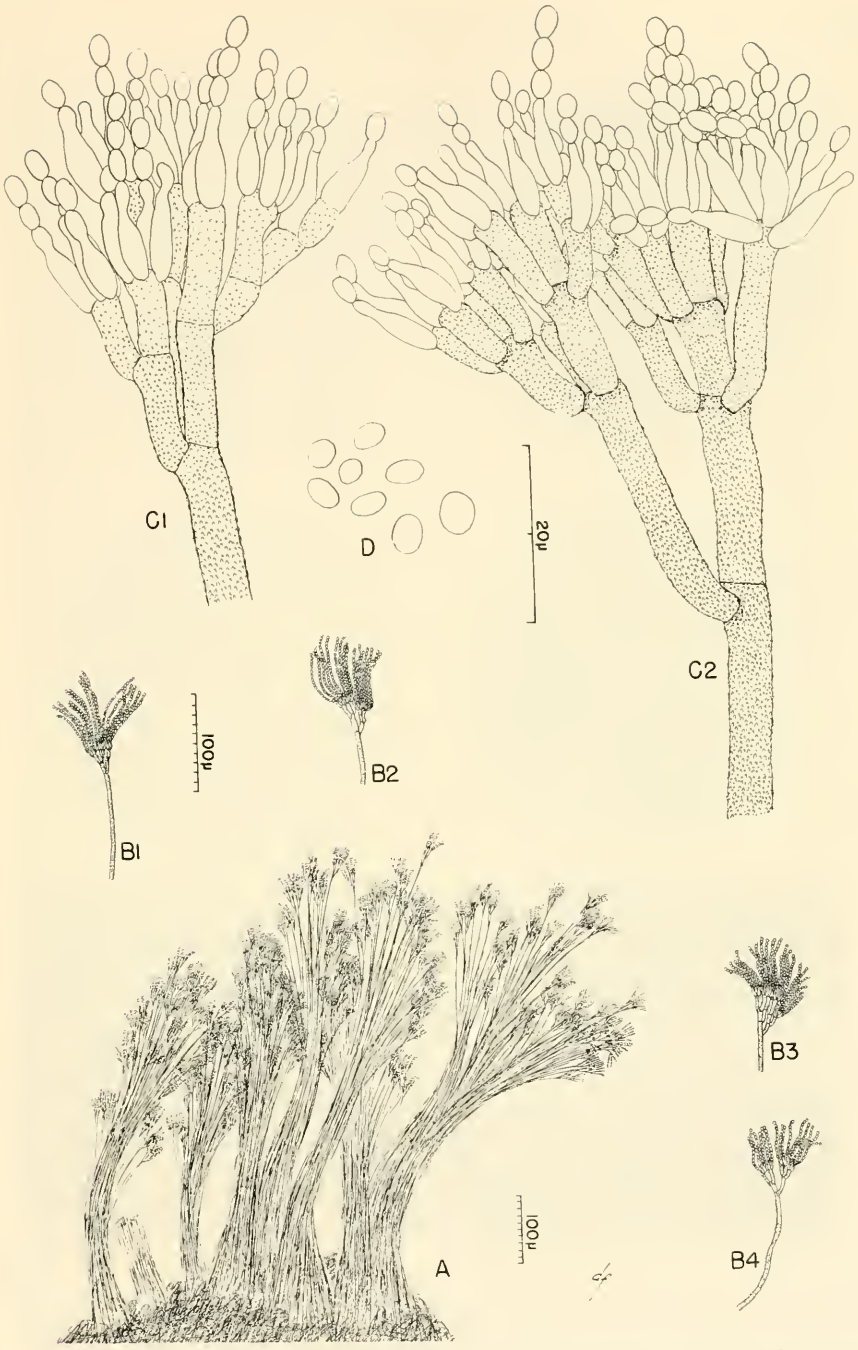


FIG. 138. *Penicillium granulatum* Bainier. *A*, Habit sketch showing characteristic fasciculate to coremiform arrangement of conidiophores. B_1–B_4, Representative penicilli as seen under low power. C_1 and C_2, Typical penicilli showing strongly granulate walls of conidiophores, branches, and metulae. *D*, Mature conidia.

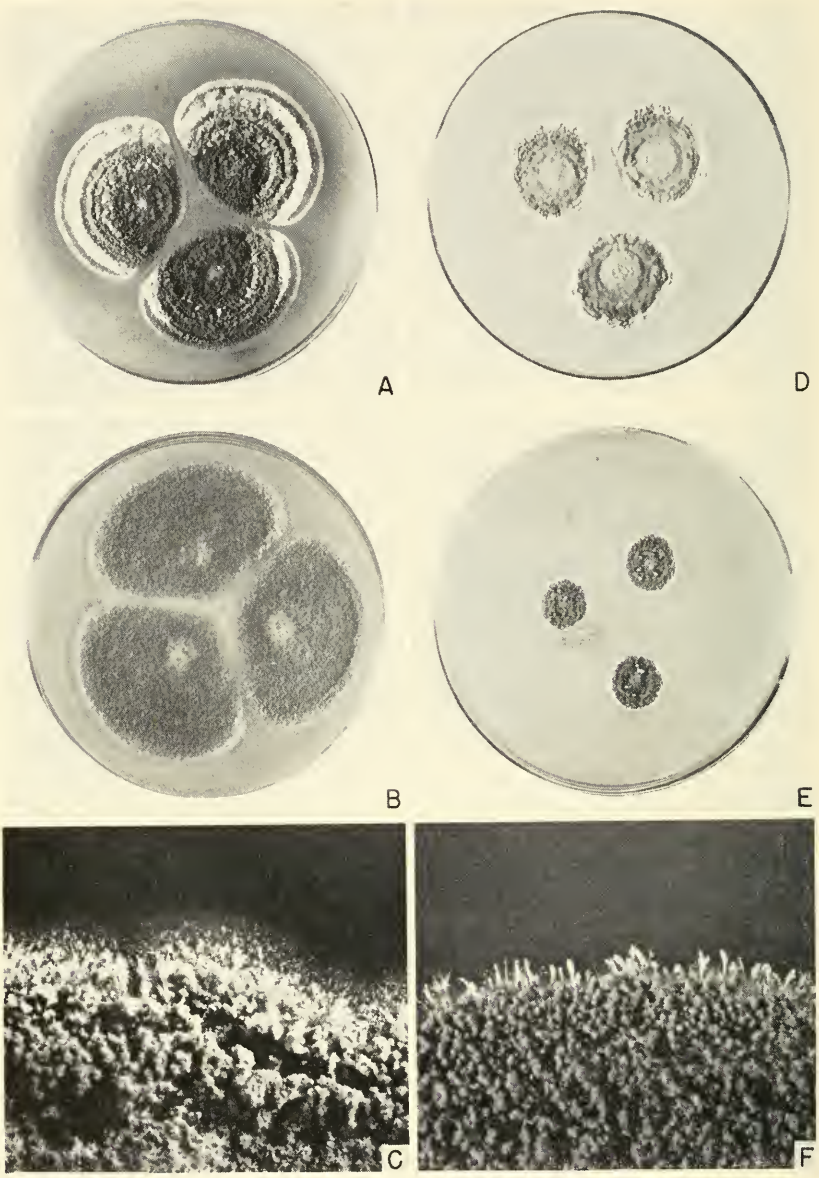


FIG. 139. *Penicillium granulatum* series. *A* and *B*, *P. corymbiferum* Westling, NRRL 2032, on Czapek and malt agars at ten days. *C*, Portion of margin from colony on Czapek, × 5. *D* and *E*, *P. granulatum* Bainier, NRRL 2036, on Czapek and malt agars at ten days. *F*, Portion of margin from colony on malt agar, × 5.

abundantly produced in most strains, usually in dark brown to maroon shades, commonly leaving distinct craters upon evaporation; odor variable,

generally not pronounced; reverse and agar becoming quickly colored in rich yellow-brown shades, less commonly pinkish or reddish brown; penicilli comparatively large, mostly 40 to 45μ in length, bearing conidia in tangled chains up to 100μ or more in length, asymmetric, comparatively regular in form, consisting of one or two appressed branches in addition to the main axis; conidiophores variable in length from 100 to 200μ or more at the margin up to 500 to 1,000μ in the strongly fasciculate central areas, 3.5 to 4.5μ in diameter, with walls closely and conspicuously roughened; branches commonly 15 to 25μ by 3.0 to 4.4μ, occasionally rebranched; metulae in groups of 4 to 6, measuring 12 to 16μ by 3.0 to 4.0μ with walls of metulae and branches usually roughened like the conidiophores; sterigmata numerous, in crowded clusters of 6 to 10, mostly 9 to 12μ by 2.0 to 2.5μ with walls apparently smooth; conidia globose to subglobose, mostly 3.0 to 3.3μ in diameter but ranging from 2.5 to 4.0μ, with walls smooth.

Colonies on steep agar spreading more rapidly, 6.0 to 7.0 cm. in 10 to 12 days with surface conspicuously granular but with fasciculation less clearly evident than on Czapek, heavily sporing throughout, with color in conidial areas as described above; exudate production less pronounced; colors in colony reverse generally in duller shades; penicilli as on Czapek but with some conidia larger and slightly elliptical.

Colonies on malt agar spreading broadly, attaining a diameter of 6.0 to 7.0 cm. in 8 to 10 days, plane except for limited floccose overgrowths in colony centers, heavily sporing throughout, conspicuously fasciculate (fig. 139B), especially in marginal areas, conidiophores 1.0 to 1.5 mm. in length, commonly appearing yellowish and with adherent orange to deep amber drops; odor usually not pronounced; penicilli as on Czapek but with conidiophores, branches, and metulae more coarsely roughened.

Species description centered primarily upon strains NRRL 2032 received in February 1946, from the Centraalbureau, as *Penicillium corymbiferum* Westling, isolated by them in 1941 from a green fly; and NRRL 999, isolated by K. J. Kadow, University of Illinois Agricultural Experiment Station in 1935, from horse radish roots, and diagnosed at that time by Thom as approximating *P. hirsutum* Dierckx.

Other strains duplicating the above have been isolated or received from collaborators periodically but, when continued in laboratory culture, usually lose certain of their characteristic features within 5 to 10 years.

Strain NRRL 996 (Thom No. 5034.64) was received in 1929 from Dr. Birkinshaw, Nobel Explosives Co., Ardeer, Scotland, and was cited by Thom in his Monograph (1930, pp. 424–425) as apparently representing Westling's species. At that time, the culture was strongly fasciculate, produced abundant drops in orange to deep red shades, and colony reverse in deep orange, reddish orange or almost black shades. This culture still produces penicilli characteristic of the species. Colonies, however, are

fairly thin, with fasciculation evident but not pronounced; exudate is lacking or very limited in amount and almost colorless; and colonies in reverse never develop the dark shades described above.

Strain NRRL 997 was received from George Smith, London School of Hygiene and Tropical Medicine, in 1935 as *Penicillium corymbiferum* and was then regarded by the authors as typical of this species. The culture now is essentially like our current stock of NRRL 996 as described above.

Strain NRRL 998, received in 1925 from Miss Clara Pratt, Imperial College, South Kensington, London and long maintained in the Thom Collection as No. 4811Z, shows a similar reduction in exudate production, in intensity of color in colony reverse, and in the degree of fasciculation. The latter culture was regarded by Thom (1930, p. 426) as possibly representative of *Penicillium hirsutum* Dierckx although he then pointed out that this species could probably not be satisfactorily separated from *P. corymbiferum*. Like NRRL 996 and 997, NRRL 998 in its present form, produces penicilli and supporting structures entirely characteristic of *P. corymbiferum*. We have no reason to question the continued purity of any of the above mentioned strains.

Strains variously diagnosed as *Penicillium corymbiferum* Westling or *P. hirsutum* Dierckx have been commonly isolated from liliaceous bulbs and root crops. They seem to represent soil forms which not uncommonly may become parasitic or semi-parasitic. The yellow-stalked fascicles suggest the yellow coremia shown among Corda's figures of his genus *Coremium*.

Penicillium hirsutum Dierckx (Soc. Scientifique Bruxelles **25**: 89. 1901) was redescribed by Biourge (Monogr., La Cellule **33**: fasc. 1, pp. 157–159; Col. Pl. II and Pl. III, fig. 18. 1923) but no satisfactory type culture was distributed by him. Thom (1930, p. 425) presented Biourge's description together with his own culture notes on certain strains which he believed to approximate the culture studied by Biourge. At that time, however, he questioned the validity of the species and suggested that it might better be regarded as a synonym of *P. corymbiferum* Westling, since Dierckx's description was hopelessly inadequate and since Biourge's redescription was antedated by Westling's. Our re-examination of the different species descriptions and comparative observation of cultures reputed to represent the two species confirm this opinion.

Penicillium granulatum Bainier, in Bul. Soc. Mycol. France **21:** 126–127; Pl. 11, figs. 5–7. 1905; Thom, U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, pp. 44–45, fig. 11. 1910; also The Penicillia, pp. 429–430, figs. 66 and 67. 1930.

Colonies on Czapek's solution agar growing rather restrictedly, approximately 2.0 to 3.0 cm. in 12 to 14 days at room temperature, comparatively deep, up to 2.0 to 4.0 mm., more or less flocculent with abundant sterile

hyphae white to dull yellow in color, surface irregularly tufted and wrinkled (fig. 139D), sporulating lightly and irregularly with conidial areas limited, in pale blue-green to glaucous green shades (Ridgway, Pl. XXXIII), conidial structures sometimes arising individually from the substratum or from the loose aerial growth but more commonly aggregated to form bundles or conspicuous coremiform fascicles (fig. 139F) from which individual conidial structures tend to diverge in the terminal portions (fig. 138A); exudate limited to abundant, clear to pale yellow; odor pronounced in most strains, fragrant, aromatic; reverse usually in dull yellow to orange-brown shades, occasionally appearing greenish in marginal areas; penicilli asymmetric, comparatively large, bearing tangled and divergent chains of conidia up to 50 to 75μ (fig. 138B), occasionally consisting of a terminal verticil of metulae, more commonly showing one or more branches somewhat appressed, with branches and the main axis bearing verticils of metulae and sterigmata; conidiophores variable in length, from 100 to 200μ up to very long in coremiform masses, approximately 3.5 to 4.0μ in diameter, with walls of conidiophores, branches, and metulae roughened, echinulate (fig. 138C); branches variable, commonly 12 to 30μ by 3.0 to 3.5μ; metulae few in the vertical, about 8 to 12μ by 3.0 to 3.5μ; sterigmata in small crowded clusters, usually about 6 to 9μ by 2.0 to 2.5μ, occasionally much longer; conidia strongly elliptical when young, in age elliptical to subglobose (fig. 138D), mostly 3.0 to 3.5μ in long axis but with individual cells frequently larger, smooth-walled.

Colonies on steep agar growing more rapidly, 4.5 to 5.0 cm. in 12 days at room temperature, essentially plane but with surface conspicuously granular from the production of abundant fascicles up to 1 mm. or more in length, heavily sporing throughout, in pale blue-green to dull gray-green shades; exudate limited in some strains, abundantly produced in others; odor generally pronounced, fragrant; reverse in drab to orange-brown shades; penicilli as on Czapek but commonly larger and in some strains with walls less definitely roughened.

Colonies on malt agar growing variously, in some strains attaining a diameter of 4.0 to 5.0 cm. in 12 days, in others restricted and not exceeding 1.5 cm. in the same period (fig. 139E); strongly fasciculate with coremia zonately arranged in some strains, commonly 2.0 mm. or more in height; odor pronounced, aromatic, fruity; penicilli as on Czapek but commonly larger and often twice-branched below the level of the metulae.

Species description centered upon NRRL 2036, isolated from soil at the Northern Regional Research Laboratory, Peoria, Illinois, in August 1942; represented also by strain NRRL 1575 from Harvard University as one of Professor Thaxter's isolates maintained as this species.

In the absence of any type material it is difficult to know exactly what

type of culture formed the basis of Bainier's description except that it was strongly coremiform, possessed granular walls, and produced conidia elliptical to globose. Thom's notes, published in 1910, from Bainier's type, defined more precisely the limits of the species but these were made from culture media seldom used in the present mycological laboratory and thus render strict interpretation difficult.

Penicillium granulatum, as the species is considered here, makes its most characteristic development upon malt extract agar. Coremia are generally larger and more clearly defined than upon other substrata; conidiophores and elements of the penicillus are more strikingly granular; and the production of odors regarded as characteristic of the species reach their maximum intensity. These odors are consistently fragrant and aromatic and are variously diagnosed as odors of over-ripe apples, cooked pineapple, mature walnut husks and occasionally a medicinal odor suggestive of a weak iodine solution.

The feathery fruiting mass that is fairly characteristic of this species results from the divergence of the individual penicilli which comprise the fascicle or coremium. In contrast, *Penicillium claviforme*, next to be considered, produces large and compact coremia in which the identity of individual conidial structures is seldom recognizable.

In general colony appearance, *Penicillium granulatum* is distinguished from *P. expansum* by much larger coremia, and by conidiophore walls that are conspicuously roughened. Strains are occasionally encountered which appear transitional between these two species. Representative of such forms is NRRL 974 received in 1922 from the Bainier Collection labelled *P. virescens*. Growing on Czapek agar, this strain is strongly suggestive of typical *P. expansum* but stalk walls are conspicuously rough. On malt agar, colonies produce more prominent coremia and conidiophores are often coarsely granular, approaching the characteristic picture of *P. granulatum*. The strain does not cause an active rot in pomaceous fruits and we believe it is more satisfactorily assigned to the latter species.

Penicillium divergens Bainier and Sartory (Bul. Soc. Mycol. France **28:** 270–276, Pl. XIII, figs. 3–6. 1912.) was described in terms which make its separation from *P. granulatum* very doubtful. Published figures of this species substantiate the basic similarity of the two forms. Since both species were described by Bainier, we can assume that some differences between the types of the two were observed. We do not believe that the differences as reported are sufficient to warrant the continued retention of both names. It is probable that they represented no more than normal strain variations which we now recognize as being characteristic of all species of Penicillia. *Penicillium divergens*, the last name proposed, is regarded as a synonym.

Penicillium schneggii Boas (Myc. Centbl. **5:** 73–83. 1914; and Centbl. Bakt. etc., (II) **44:** 695–696. 1916; also Thom, The Penicillia, pp. 415–416. 1930) was originally described in terms which clearly relate it to the *P. granulatum* series: Coremia ranged

from 2 to 12 mm. in length with green conidial masses, in age often becoming feathery and sterile; conidiophores fairly coarse, with walls granulate or punctate; penicilli once- or twice-branched and bearing verticils of metulae and sterigmata; conidia elliptical toward globose. Colony reverse ranged from yellow to reddish or red in age, and colonies were characterized by the production of some aromatic ester.

A culture (NRRL 985) derived from Boas' type, which was examined in the current study, conforms with the above description reasonably well except for an absence of large heavily sporulating coremia. Sterile feathery overgrowths are occasionally produced as reported by Boas and as confirmed by Thom (1930, p. 418), and colonies regularly produce an aromatic odor approximating, if not actually duplicating, that of typical *Penicillium granulatum* strains such as NRRL 2036 and 1575. Furthermore, colonies on malt agar often tend to become strongly fasciculate in age and to develop reddish or red shades as described originally by Boas, and as sometimes seen in our cultures of *P. granulatum*. The culture in question exhibits strain individuality that has been successfully preserved (in part) for more than thirty years in laboratory culture; nevertheless, we do not believe that it differs from *P. granulatum* sufficiently to warrant retention of the species.

Occurrence and Significance

Penicillium corymbiferum Westling and *P. granulatum* Bainier appear to be widely distributed but not particularly abundant in soils. Representatives of both species have been isolated from decaying vegetation also, but their role in decomposition processes has not been investigated.

Penicillium corymbiferum commonly appears on bulbs and fleshy root-stocks, and may under some conditions become actively parasitic. Van Beyma (1928c) isolated the species repeatedly from tulip bulbs in Holland, and in some cases found them to be entirely covered and permeated with the mycelium of the fungus. Weber (1932) reported a similar infection of tulip, hyacinth, and narcissus bulbs in Denmark, attributing the disease to *P. corymbiferum*. Ghamrawy (1933) isolated the same species of *Penicillium* from Cape hyacinth bulbs (of Dutch origin) in a warehouse in London. Inoculation experiments showed that *P. corymbiferum* alone was capable of rotting bulbs when planted in soil. Infection appeared to occur through wounds. Moore (1943) isolated from *Scilla* bulbs a *Penicillium*, identified by George Smith as belonging to the *P. corymbiferum-hirsutum* group.

Kadow and Anderson (1940) found a *Penicillium*, identified as *P. hirsutum* (see above), to cause a serious root-rot of horse-radish in Illinois. Control was effected by dusting the harvested root-stocks with sulphur. Böning (1936) had earlier reported a *Penicillium* disease of horse-radish in Germany, but failed to identify the pathogen.

The chemistry of aromatic substances produced by *Penicillium granulatum* and *P. expansum* was investigated by Blinc and Krivic (1940) and these appeared to be due to esters of unsaturated fatty acid.

Penicillium granulatum was reported by Dalvi (1930) to represent one

of the Penicillia commonly found in the microflora of tan-liquors in Bangalore, India. The species is often cited in the older literature, but actual significance was seldom established. It has not been investigated biochemically.

Penicillium claviforme Series

Outstanding Characters

Large, conspicuous coremia regularly produced, often zonately arranged, characterizing the colony upon most substrata, but with separate penicilli occasionally developed from either submerged or floccose aerial hyphae.

Conidiophores arising primarily from the substratum, often up to 2 to 3 mm. or more in length, closely interwoven to form a fibrous stalk in which the identity of individual structures is lost, or more loosely aggregated with conidiophores closely adherent but retaining their individuality, smooth-walled.

Penicilli typically large, asymmetrical, and often very irregular with parts commonly interlaced with those of adjacent structures to form a continuous spore bearing surface suggestive of an hymenial layer. All parts smooth-walled.

Series Key

2. Coremia prominent, with simple conidiophores few in number or lacking; conidiophore walls smooth..... *P. claviforme* series
   a. Coremia typically club-shaped and showing clear differentiation into a compact fibrous stalk and an expanded "sporehead" composed of massed and interwoven penicilli..... *P. claviforme* Bainier
   b. Coremia typically loose in texture (Isaria-like), often not clearly differentiated into stalk and "sporehead"; commonly appearing feathery with penicilli usually separate..... *P. clavigerum* Demelius

Two species are recognized, as follows: *Penicillium claviforme* Bainier and *P. clavigerum* Demelius. The first of these has long been recognized, and without doubt represents one of the most striking members of the genus. It was described by Bainier in 1905 and illustrated with sufficient skill to insure its subsequent identification. Saccardo recognized the species and included it in his Sylloge in 1906. Subsequent to this, Wehmer (1914) described the same fungus as *Coremium silvaticum*. Examination of his type culture (now maintained as NRRL 1001) revealed certain fairly distinctive characteristics but failed to show significant differences to separate it from Bainier's culture and prior description of *P. claviforme*. Both Biourge (1923) and Gaümann (1926) properly removed the species from *Coremium* and placed it in the genus *Penicillium*, but neither recognized its identity with *P. claviforme*. This relationship was subsequently clari-

fied by Thom (1930). *Penicillium claviforme*, as the name suggests, is characterized by club-shaped coremia. In its typical aspect these are clearly differentiated into a compact, fibrous stalk 1 to 2 mm. or more in length and 250 to 400μ or more in diameter, terminated by an expanded and typically rounded "sporehead" in which tremendous numbers of penicilli become intimately interlaced to produce a continuous spore (conidium) bearing surface. Chains of conidia, remaining parallel and adherent, develop from this sterigmatic layer and tend to separate into broad columnar masses as they increase in length, with the result that the mature sporeheads commonly appear deeply and irregularly dissected (fig. 140B). Not infrequently conidial structures may be aggregated into palisade-like masses rather than collected into the typical and separate coremia that characterize the species. When grown in one-sided illumination the coremia are markedly phototropic, longer, and often spatulate rather than rounded. In extreme cases they may become strongly dissected with conidial areas limited to the outermost tips of the branching structures. Similar dissected coremia often develop in marginal areas of aging colonies after two or three weeks.

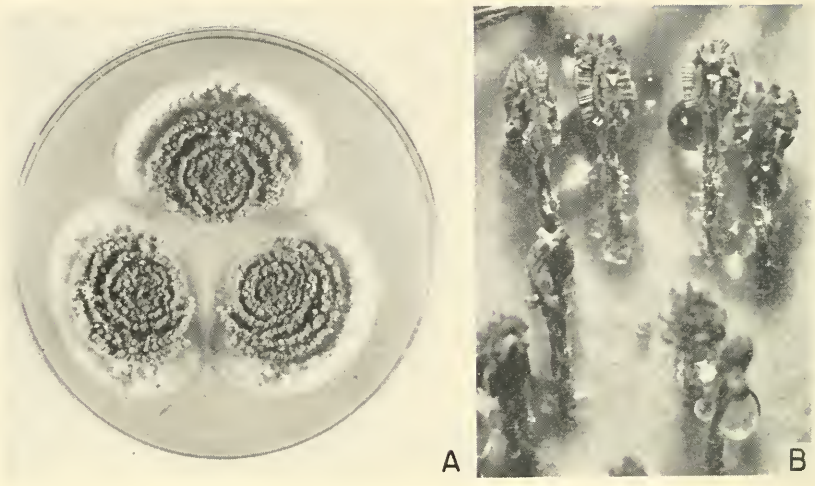
Penicillium clavigerum, as the species is regarded here, is believed to be closely related to *P. claviforme*. Colonies normally present a strongly coremiform aspect, conidiophores are smooth-walled and penicilli are large, asymmetric, and usually branched. Unlike the coremia of *P. claviforme*, which typically show a clear differentiation into sterile supportive stalks and enlarged sporeheads, the coremia of *P. clavigerum* are of looser texture and are more nearly uniform in diameter throughout. Although conidial heads are generally concentrated in the terminal portion of the coremia, they may be borne over the greater portion of their entire length. The coremia often appear more or less feathery and in some measure suggest the structures seen in the *P. granulatum* series; they differ from these, however, in their greater length and more compact nature, and in being composed of smooth rather than conspicuously rough-walled conidiophores.

Penicillium claviforme Bainier, in Bul. Soc. Mycol. France **21:** 127, Pl. XI, figs. 8–11. 1905. Saccardo, Sylloge Fung. **18:** 520. 1906. Thom, U. S. Dept. of Agr., Bur. Anim. Ind., Bul. 118, p. 44, fig. 10. 1910; and The Penicillia, pp. 432–433, fig. 68. 1930

Synonyms: *Coremium claviforme* (Bainier) Peck, in New York State Museum Bul. 131, p. 16, 1909.

Coremium silvaticum Wehmer, in Ber. Deut. Bot. Ges. **31:** 373–384. 1914.

Penicillium silvaticum (Wehmer) Biourge, in Monograph, La Cellule **33:** fasc. 1, p. 105. 1923.



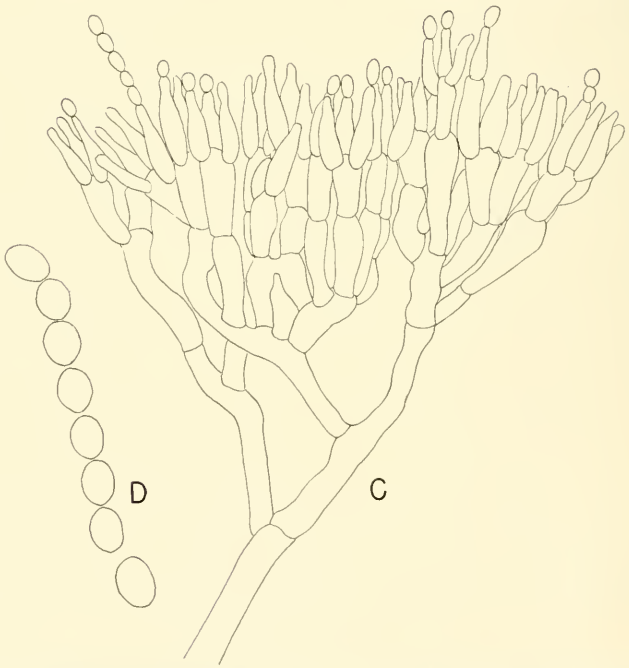


FIG. 140. *Penicillium claviforme* Bainier. *A*, Two-week old colonies of NRRL 2149 on steep agar. *B*, Enlarged view of coremia in strain NRRL 1002, × 5. *C*, Large and much branched "penicillus" (see text) in strain NRRL 2031, × 750. *D*, Mature conidia, × 1600.

Penicillium silvaticum (Wehmer) Gaümann, in Vergl. Morph. Pilze, p. 177, fig. 113. 1926.

Coremium vulgare Corda, in Prachtflora, 1839. Part but not all of figs. in Pl. XXV may be this species.

Colonies on Czapek's solution agar attaining a diameter of 2.5 to 3.0 cm. in 12 to 14 days at room temperature with vegetative mycelium white to light grayish, largely submerged in some strains, partially aerial and floccose in others with this floccose hyphae commonly bearing separate penicilli loosely scattered; species particularly characterized by the production of large and conspicuous coremia, commonly in concentric zones, with coremium stalks compact, fibrous, from white to flesh color or rose, simple, flattened or variously branched, commonly measuring 2 to 3 mm. in height but occasionally up to 1 cm. or more, and terminated by a clavate, spatulate, or divided mass of conidial structures, in some cases composed of well-differentiated asymmetric penicilli on tangled and interwoven conidiophores, but more commonly with individual fruiting structures less well-defined and sterigmatic elements interlaced to produce a hymenium-like spore-bearing surface, with the entire terminal area covered by crowded conidial chains which separate into broad irregular columns up to 500μ or more in length in age, in color approximating Russian green (Ridgway, Pl. XLII) to sage green (R., Pl. XLVII); odor very strong, penetrating, pungent, to some individuals suggesting Irish potatoes in storage, to others more or less aromatic; exudate abundantly produced in some strains, collecting into large, crystal clear drops, generally adherent to the stalks; reverse brown in age, darker directly beneath the coremia; penicilli very irregular (fig. 140C), often large or individually indistinguishable with elements closely crowded and interlaced to form a continuous spore bearing surface; conidiophores poorly defined, with walls smooth, about 3.5 to 4.0μ in diameter; branches, when distinguishable, range from 10 to 25μ or 30μ by 3.0 to 4.0μ; metulae occur singly or in groups of 2 to 4, ranging from incurved to strongly divergent; sterigmata few to the metula, mostly 9 to 12μ by 2.0 to 2.8μ; conidia elliptical, 4.0 to 4.5μ by 3.0 to 3.5μ with walls smooth (fig. 140D), commonly adherent in long chains in fluid mounts.

Colonies on steep agar essentially as described on Czapek but larger, 5.0 to 6.0 cm. in diameter in 2 weeks (fig. 140A) and with coremia averaging slightly larger, with exudate production, odor, colony reverse, and conidial structures duplicating the above.

Colonies on malt essentially as on Czapek but with coremia less numerous and with stalks generally longer (fig. 141) and more definitely red in color, with other characters as already described.

Species description based upon the following strains: NRRL 1002 from

the Thom Collection (No. 4733.39.1), originally from Biourge as *Penicillium claviforme* Bainier; NRRL 2031, received in February 1946 from the Centraalbureau as the same species; NRRL 2149 from Dr. G. A. Ledingham, National Research Council, Ottawa, Canada, as an unnamed species from Firma Konig Lubek, Germany; and NRRL 1001 from Wehmer in 1922 as his *Coremium silvaticum* (see synonyms above). The latter culture differs from the other four in producing less well-defined coremia which are commonly joined by vegetative hyphal bridges. The character of the sterigmatic surface, the size and form of the conidia, and the color of mature

FIG. 141. *Penicillium claviforme* Bainier, NRRL 2031, on malt agar at two weeks.

conidial masses, however, are identical in the different strains and there is little question but that NRRL 1001 represents merely a variant of Bainier's species.

The type culture was given to Thom in 1905 by Bainier when Thom visited his laboratory in Paris. It was long maintained in the latter's Collection as No. 4640.441 and was cited as such in Thom's discussion of this species in his Monograph (1930). Re-examination of original culture notes made by Thom indicate that this culture duplicated, in all particulars, NRRL 1002 and 2031 examined in the current study.

Penicillium claviforme Bainier is perhaps the most striking member of the genus and, once observed, cannot easily be mistaken. Apparently, the species is not common in nature for few original isolations have been reported.

Strains of *Metarrhizium anisopliae* (Metschnikoff) Sorokin are occasionally isolated from insects or soil in which the massed conidial structures (typically forming sporodochia) bear a limited resemblance to the coremia of *Penicillium claviforme*, particularly when the latter are connected by bridges of aerial hyphae. *Penicillium anisopliae* (Metsch.) Vuillemin, sometimes considered in relation to *P. claviforme* Bainier, is in reality not a *Penicillium* but a *Metarrhizium* (see p. 22).

Penicillium clavigerum Demelius, in Verhandl. Zool.-Bot. Gesellsch. Wein **72:** 74–75, fig. 4. (1922) 1923

Colonies on Czapek's solution agar growing rather restrictedly, attaining a diameter of 3.0 to 4.0 cm. in 10 to 12 days at room temperature, very strongly fasciculate throughout with the coremiform aspect dominating the entire colony (fig. 142A); coremia *Isaria*-like, simple (fig. 142C), rounded, or more or less flattened and even spraying out into a number of sporulating tips, variable in length up to 3 or 4 mm.; simple coremia commonly of uniform diameter throughout with apices usually pointed and with penicilli more concentrated in terminal portions, but generally borne over their entire length; coremia seldom clavate and rarely showing a clear differentiation into stalk and spore bearing areas, white at first but developing dull yellow-green shades near slate olive (Ridgway, Pl. XLVII) when mature and finally deep slate olive in age; exudate limited, lightly colored, borne near the agar surface and often obscured by the developing coremia; odor pronounced, moldy; reverse quickly becoming dull pinkish brown, darkening in age; penicilli abundantly produced, borne primarily upon sinuous and interlacing conidiophores (fig. 142D) which comprise the body of the coremium; conidiophores variable in length, mostly very long up to several millimeters by 3.5 to 4.0μ in diameter, with walls smooth; penicilli asymmetric, commonly showing one or two branches (fig. 142D) in addition to the main axis, but not infrequently bearing a single terminal verticil of metulae; branches mostly 10 to 15μ by 3.5 to 4.0μ; metulae usually in groups of 2 to 4 measuring 8.0 to 12μ by 3.0 to 3.5μ, slightly inflated at the apices; sterigmata crowded, commonly borne in clusters of 6 to 10, mostly 7.0 to 9.0μ by 2.0 to 2.5μ gradually tapered to conidium bearing tips in a manner suggestive of the Biverticillata-Symmetrica; conidia elliptical 3.0 to 4.0μ by 2.2 to 3.0μ, with walls smooth.

Colonies on steep agar as described above except conidial areas quickly becoming dark, approaching dull greenish black (R., Pl. XLVII) in 10 to 12 days, abundant slime produced and conidial chains becoming wet, com-

pacted, and dark; odor as described above; reverse in dark walnut to almost black shades; penicilli with parts generally as described above but usually more complexly branched.

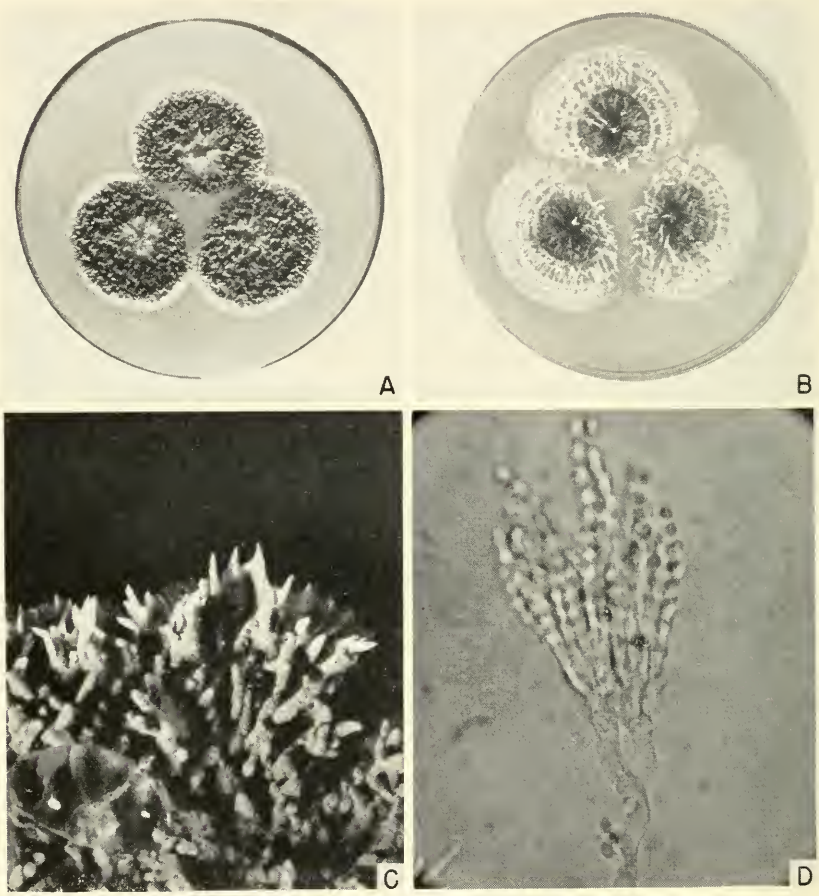


FIG. 142. *Penicillium clavigerum* Demelius, NRRL 1003. *A* and *B*, Ten-day-old colonies on Czapek and malt agars. *C*, Enlarged view of colony margin as seen on steep agar, × 5. *D*, Detail of a penicillus, × 750.

Colonies on malt agar generally as described above, but with coremia less abundant, often longer and more strongly branched (fig. 142B), usually lighter sporing; penicilli generally larger and more complexly branched, with parts somewhat thinner than on Czapek.

Species description based upon NRRL 1003 received from Dr. G. R. Bisby, Winnipeg, Canada, in 1934. Represented also by NRRL 1004 re-

ceived in 1939 from Dr. C. W. Emmons, National Institute of Health, Washington. The latter strain differs only in producing less heavily sporing colonies and conidia that are somewhat smaller and less consistently elliptical.

Assignment of the above strains to Demelius' *Penicillium clavigerum* is based upon a number of considerations, including: comparatively large, asymmetric, branched penicilli; coremia up to 3 mm. or more in length; smooth-walled conidiophores; and elliptical smooth-walled conidia 3.0 to 4.0μ by 2.3 to 3.0μ. These strains differ from her description in developing yellow-green to olive rather than blue to gray-green shades; in exhibiting a less clear cut differentiation into supportive stalks and terminal conidial areas; and in producing conidiophores that are colorless or nearly so in contrast to yellow as reported by her. Her figures of the penicillus and the coremium, though somewhat diagrammatic, are fairly representative of the strains we have assigned to this species. Exact duplication of the above strains with Demelius' culture is not claimed, and it is possible that they should be regarded as representing a new species. However, consistent with our practice of not introducing a new name if a published species can be regarded as reasonably representative, we have elected to assign these cultures to *P. clavigerum*. In the present case, points of similarity are believed to definitely outweigh points of difference, especially since these latter, *e.g.*, colony color and coloration of coremia stalks, may be strongly influenced by the substratum.

A strain received from the Centraalbureau in February 1946 under this name, as an isolate from canvas made in 1939, produces coremia of the general type described and figured by Demelius, but the penicilli are typically biverticillate and symmetrical. This culture adequately represents *Penicillium duclauxi* Delacroix and is further considered under the discussion of that species.

Occurrence and Significance

Members of the present series occur as infrequent components of the mycoflora of soils.

Penicillium claviforme Bainier has attracted considerable attention recently as a producer of an antibiotic that is variously referred to as claviformin, patulin, clavacin, etc. (see p. 537). Chain, Florey, and Jennings reported the production of this antibiotic by *P. claviforme* in 1942. We feel that the name claviformin, which they applied to it, should be adopted since they were the first to obtain the substance in crystalline form. While quantitative comparisons have not been conducted, tests performed at this Laboratory would seem to indicate that strains of *P. claviforme* are more productive of the antibiotic than other organisms reported to produce it.

The production of an antibiotic, unidentified but probably representing claviformin, by *P. claviforme* was reported by Wilkins and Harris (1945). Lochhead, Chase, and Landerkin (1946) reported the production of claviformin by soil Penicillia (unidentified as to species) and described methods for the assay and extraction of the antibiotic.

Penicillium silvaticum (synonym of *P. claviforme*) is occasionally included among the soil fungi reported by different authors. No particular significance has been attached to its presence.

No biochemical studies have been reported for *Penicillium clavigerum* Demelius.

Chapter XIII

BIVERTICILLATA-SYMMETRICA

Wehmer (1914) and Thom (1915a and b) each described the symmetrically biverticillate type of penicillus as the outstanding common character for a major natural group of Penicillia. Wehmer proposed to call this section of the genus the Verticillatae, without designating it as a subgenus. Thom referred to it as the *Penicillium luteum-purpurogenum* group. Biourge (1923) subsequently applied to it the name *Biverticillium* and called the section a subgenus. *Penicillium purpuogenum* Fleroff-Stoll was given as the first species and his discussion clearly indicated that the type of structure found in the Luteum-Purpurogenum Group of Thom, or the Verticillatae of Wehmer, represented in a general way Biourge's idea of *Biverticillium*. However, he went on to include *P. aurifluum* Biourge (*P. citrinum* Thom), *P. atramentosum* Thom, *P. flexuosum* Dale (*P. urticae* Bainier), and *P. fellutanum* Biourge—species which could not possibly belong with *P. purpurogenum*. The idea of a subgenus *Biverticillium* had to be discarded.

Later, the long lanceolate sterigmata of the "luteum" type of *Penicillium* was found to represent a more general and more definite character even than the symmetrical biverticillate penicillus. Thom (1930), therefore, proposed this as the principal identifying character of an entire section, which he designated the Biverticillata-Symmetrica in recognition of the typical penicillus pattern. Subsequent investigations have confirmed the merit and usefulness of these distinguishing characters. Series of species in the Velutina and the Divaricata with penicilli commonly biverticillate but asymmetrical and lacking the characteristic lanceolate sterigmata are thus readily excluded.

The conidiophore of this group typically produces a simple terminal, symmetrical whorl, or verticil, of 4 or 5 to several metulae, each of which bears a symmetrical verticil of closely packed sterigmata. The main axis prolonged usually forms the central metula. This prolongation of the main axis occasionally produces a secondary or superimposed verticil of metulae, and less frequently secondary verticils of metulae arise from the tips of other primary metulae. In marked contrast to such rebranched penicilli, monoverticillate or fractional structures are occasionally present in almost all species, and more or less characterize some species and strains which otherwise clearly belong within the Biverticillata-Symmetrica Section.

The typical sterigma of the group is a comparatively slender tube with

the apical portion tapering to a long acuminate point (see fig. 11C) from which the conidia are usually cut off as long cylindrical segments.

In most forms the conidia are at first cylindrical, usually swell quickly in the center, and commonly assume fusiform to elliptical shapes—in some species becoming globose or nearly so. The cell wall may be smooth, or roughened as a varietal or species character.

The whole aspect of the penicillus is so characteristic that once it is well understood, the large majority of the members of the group can be allocated to it at once from examination under the lower objectives of the compound microscope.

There is considerable evidence that species with symmetrically biverticillate penicilli and typically lanceolate or acuminate sterigmata constitute a natural and homogeneous group. Nearly all of the strains encountered produce yellow to orange or reddish colors in the aerial vegetative mycelium, and yellow through orange to deep red in the substratum. These colors, and their transformations within the particular culture, may develop quickly or slowly, and are usually intensified upon some media and more or less suppressed on others. In culture media containing fermentable sugars in the presence of inorganic nitrogen, peptone, or steep liquor most of these species quickly produce a pronounced and often characteristic coloration. Thom (1930) reported the colors of *P. duclauxi* Delacroix, as diffused in the substratum to be yellow in acid and red under alkaline conditions and to be reversible with approximately the same relation to acid and alkali as phenolphthalein. The hyphae comprising the aerial mycelium usually appear granular or encrusted when viewed dry under low magnifications, and it is this superficial pigmented material in massed hyphae which is primarily responsible for the bright yellow to orange coloration of entire or limited colony areas in some species. In other species the encrusted hyphae are less abundant and more diffuse, often lending a pronounced yellow cast to otherwise dark green or dull green conidial areas.

Deceptive appearances may in some instances lead to an arbitrary and erroneous allocation of species. Nevertheless, Penicillia can almost invariably be placed here if they produce (1) biverticillate conidial structures which are usually symmetrical, (2) lanceolate or acuminate sterigmata with long-tapered conidium-bearing tubes, (3) aerial hyphae more or less yellow pigmented and encrusted, and (4) colony reverse in yellow, orange, or red to purplish red shades. In addition to these forms, there are occasional species which demonstrate certain of the above characteristics with unmistakable clarity, yet fail to show others usually regarded as equally diagnostic. For example, members of the *Penicillium herquei* series develop biverticillate penicilli that are essentially symmetrical and

often show abundant yellow encrusted vegetative hyphae, yet fail to produce sterigmata of characteristic pattern and develop a yellow to bright green or dark green rather than yellow to red pigmentation in the colony surface and reverse with Czapek's agar.

Certain species such as *Penicillium vermiculatum* Dangeard, *P. wortmani* Klöcker, etc. that are consistently perithecial, develop conidial structures entirely typical of the section (fig. 143B) and hence are included. Usually these develop yellow or orange rather than red pigmentation in areas of heavy mycelial development and in the colony reverse. Other perithecial forms, obviously closely related, *e.g.*, *P. stipitatum* Thom, tend to produce fractional penicilli but show sterigmata (fig. 143A) and yellow encrusted hyphae characteristic of the group. Still another, *P. avellaneum* Thom and Turreson, produces large, coarse penicilli hardly suggestive of the section (fig. 143C), but develops perithecia and an abundance of yellow encrusted mycelium strikingly like the above, hence is included here.

The true relationships between perithecial and strictly conidial forms are generally obscure. Not infrequently, asexual strains have been observed to originate in culture by a gradual and progressive reduction in perithecium formation. More often, however, members of the section are strictly conidial when isolated, and we can only speculate regarding their possible origin in nature and their possible identity as unisexual haplonts. Attempts to develop perithecial forms by growing such asexual strains in pairs have proved unsuccessful. Yet, they often resemble so closely the conidial phase of known perithecial species that close relationship, if not actual identity, may be presumed.

The non-ascosporic members of the Biverticillata-Symmetrica are subdivided into five series, primarily upon the bases of colony texture and coloration, as shown in the accompanying key. These are centered around *P. duclauxi* Delacroix, *P. funiculosum* Thom, *P. purpuogenum* Stoll, *P. rugulosum* Thom, and *P. herquei* Bainier and Sartory, as the most abundant and representative species in the different series. Identification to species in this, as in other sections, is often difficult, but assignment to series is usually readily accomplished. Fortunately, identification to series is sufficiently accurate for many types of investigations.

A few species produce sclerotia. In all cases these are fairly irregular in pattern and dimensions and appear to be less highly organized than those seen in the *Penicillium thomii*, *P. raistrickii*, and *P. gladioli* series. They consist of irregular masses of comparatively large polygonal cells with walls somewhat thickened and dark-colored, usually in deep reddish brown, brownish black, or greenish black shades. Unlike the sclerotia of series in other sections which are produced upon the agar surface, these are often partially embedded within the substratum.

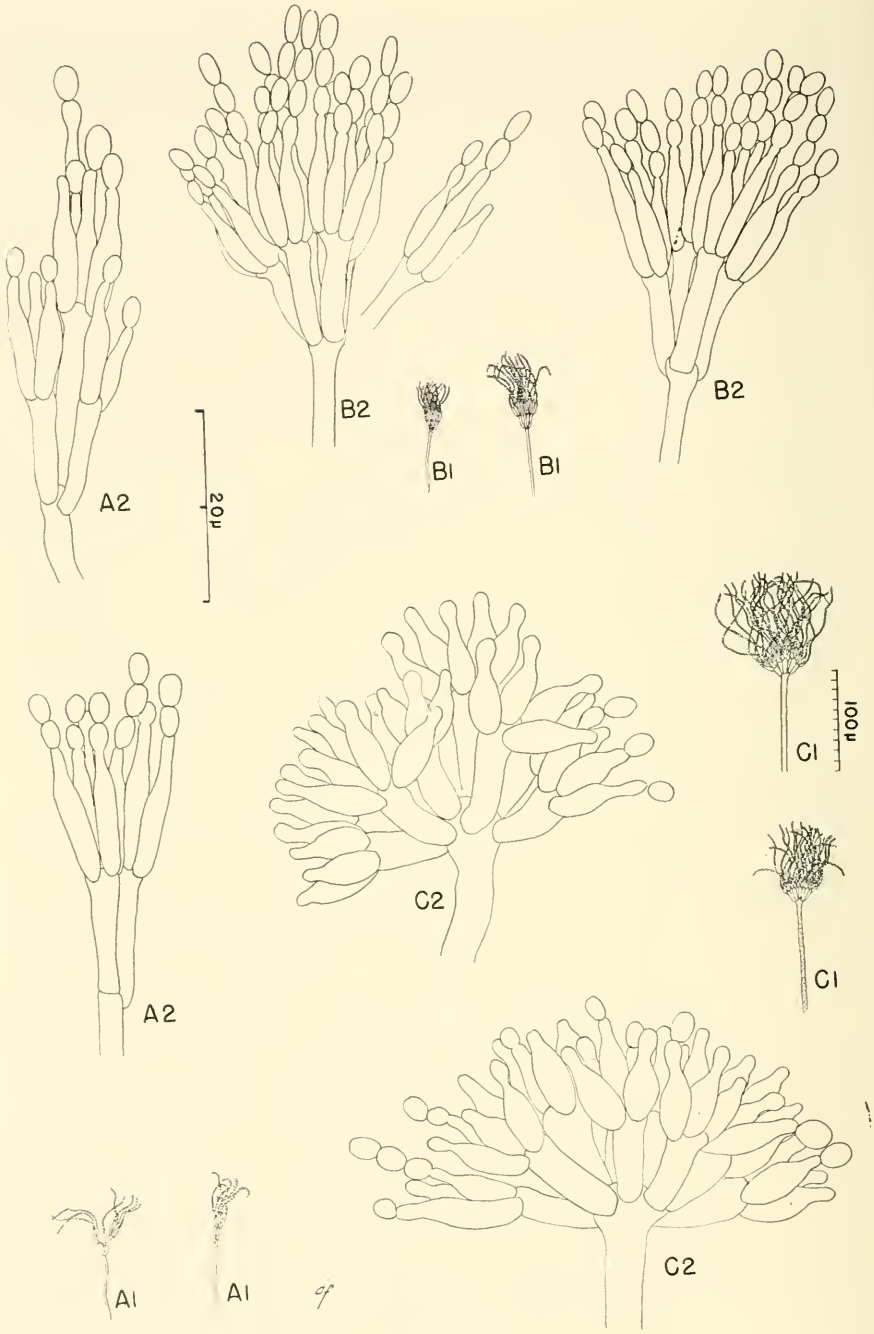


Fig. 143

Key to the Biverticillata-Symmetrica

Page

I. Colonies typically producing perithecia or sclerotia.
  A. Colonies producing soft perithecia upon most substrata, usually in bright yellow (*luteus*) shades ..... *P. luteum* series 564
    1. Ascospores usually with prominent equatorial ridges.
      a. Strains typically thermophilic; colonies pale salmon colored to dull grayish green ..... *P. duponti* Griffon and Maublanc emend. Emerson 573
      b. Strains not thermophilic; colonies typically bright yellow to greenish yellow ..... *P. stipitatum* Thom 577
    2. Ascospores without definite equatorial ridges.
      a. Ascospore spinulose over their entire surface; asci borne in chains.
        1′. Ascospores elliptical.
          aa. Perithecia in bright yellow, golden yellow or orange-yellow shades.
            1″. Ascospores 4.0 to 5.0μ in long axis.
              aaa. Perithecial initials enlarged, long, clavate, unbranched; colonies spreading broadly. *P. vermiculatum* Dangeard 580
              bbb. Perithecial initials irregularly enlarged, septate and often branched; colonies somewhat restricted ..... *P. wortmanni* Klöcker 583
            2″. Ascospores seldom exceeding 3.0μ in long axis; perithecial initials long, helicoid; colonies spreading broadly ..... *P. helicum* Raper and Fennell 586
          bb. Perithecia in white to cream or light yellowish shades; perithecial initials conspicuously swollen, often becoming branched ..... *P. spiculisporum* Lehman 589
        2′. Ascospores globose.
          aa. Conidia elliptical with ends somewhat pointed; perithecia in golden-yellow to orange-yellow shades. *P. rotundum* Raper and Fennell 591
          bb. Conidia bacilliform, rod-like; perithecia typically in pale yellow shades ..... *P. bacillosporum* Swift 594
      b. Ascospores not spinulose over their entire surface; asci borne singly as short branches from fertile hyphae.
        1′. Ascospores with walls pitted; perithecia in bright yellow shades; conidial heads in avellaneous shades. *P. avellaneum* Thom and Turesson 597

FIG. 143. Conidial structures in different members of the *Penicillium luteum* series. A_1, Habit sketches of penicilli in *P. stipitatum* Thom; A_2, Camera lucida drawings showing the irregular pattern and apparently fractional character of penicilli of the same species. B_1, Habit sketches of penicilli in *P. wortmanni* Klöcker; B_2, Detailed drawings of the same, showing the symmetrically-biverticillate character of penicilli and the lanceolate pattern of sterigmata which together characterize the Biverticillata-Symmetrica. C_1, Penicilli of *P. avellaneum* Thom and Turesson as seen under low power; C_2, Camera lucida drawings showing the pattern and cellular arrangements in penicilli of the same species. Neither the general pattern of the penicillus nor the character of the sterigmata in the latter species are typical of the section, but the ascosporic stage is regarded as placing *P. avellaneum* in the Biverticillata-Symmetrica.

Page

2′. Ascospores with conspicuous transverse (spiral) bands ("tricostate" of Zukal); perithecia in bright yellow shades.
P. luteum Zukal 600

3′. Ascospores with multiple longitudinal ridges; perithecia white or cream colored..... *P. striatum* Raper and Fennell 603

B. Colonies producing sclerotia in greater or less abundance upon most substrata.

1. Sclerotia in dark red or blackish shades, often elongate; penicilli typically biverticillate and symmetrical.

a. Sclerotia dark red or reddish black in color, usually more or less rounded and borne upon the substratum.
P. purpurogenum var. *rubri-sclerotium* Thom 636

b. Sclerotia black, brownish black, or greenish black, usually elongate, often more or less embedded in the substratum.

1′. Sclerotia abundantly produced, often characterizing the culture; conidiophores and metulae conspicuously roughened.
P. novae-zeelandiae v. Beyma 665

2′. Sclerotia sparsely and tardily produced in occasional strains; conidiophores and metulae smooth-walled or nearly so.
P. funiculosum Thom 616

3′. Sclerotia reported; conidiophores long and comparatively coarse, usually rough-walled, at least in the terminal area.
P. herquei series 658

2. Sclerotia in light cream to yellow shades, rounded; penicilli biverticillate, sometimes appearing symmetrical.
P. raistrickii Smith and allied species
(in the Divaricata, p. 255)

II. Colonies not producing perithecia or sclerotia.

A. Colonies regularly developing abundant, erect coremia, often characterizing the culture.

1. Penicilli typically biverticillate and symmetrical; sterigmata lanceolate, with tips gradually tapered; colonies developing yellow-orange or red shades in reverse..... *P. duclauxi* series 609
P. duclauxi Delacroix 610

2. Penicilli typically asymmetrical; sterigmata with tips more abruptly narrowed; colonies seldom developing true red shades in reverse.
P. claviforme series
(in the Fasciculata, p. 548)

B. Colonies seldom or never developing true coremia.

1. Colonies with surface appearing funiculose, floccose-funiculose, or somewhat tufted; conidiophores arising primarily from aerial hyphae or ropes of hyphae..... *P. funiculosum* series 614

a. Conidial chains tangled or divergent; metulae parallel or somewhat divergent.

1′. Colonies usually spreading broadly upon most substrata.

aa. Conidia elliptical to subglobose, smooth or nearly so; reverse in pink to deep red or orange-brown shades, occasionally almost black..... *P. funiculosum* Thom 616

Page

bb. Conidia globose, conspicuously echinulate; reverse uncolored or in pale drab to greenish shades, becoming dull brown in age ..... *P. verruculosum* Peyronel 621

2′. Colonies usually more or less restricted upon most substrata.

aa. Conidia elliptical, heavy-walled, smooth; conidiophores uncolored; colonies bristly, showing areas of red, orange, or yellow mycelium and dark green conidia. *P. islandicum* Sopp 623

bb. Conidia ovate to elliptical, thin-walled, smooth; conidiophores heavy-walled, dull yellow-green; colonies fibrous to floccose or floccose-funiculose, mostly in buff to orange-pink shades ..... *P. varians* Smith 625

b. Conidial chains forming a conical or pyramidal mass; metulae numerous, incurved ..... *P. piceum* Raper and Fennell 627

2. Colonies with ropiness absent, or reduced and inconspicuous, typically velvety or lanose; conidiophores arising primarily from the substratum or from the basal felt.

a. Colonies on Czapek and steep agars usually developing an intense red or purple-red pigmentation; commonly producing aromatic odors suggesting apples or walnuts on malt agar. *P. purpurogenum* series 631

1′. Colonies consistently producing deep red colors in reverse; surface usually heavy sporing and showing an evident but limited development of yellow or orange-red aerial hyphae.

aa. Conidia elliptical to subglobose; penicilli comparatively long, sterigmata closely parallel; pigmentation diffusing throughout the surrounding agar.

1″. Conidia typically roughened; colonies sometimes spreading; conidial areas in dark yellow-green shades. *P. purpurogenum* Stoll 633

aaa. Producing sclerotia, at least when newly isolated. *P. purpurogenum* var. *rubri-sclerotium* Thom 636

2″. Conidia smooth; colonies more restricted; conidial areas in lighter yellow-green to gray-green shades. *P. rubrum* Stoll 637

bb. Conidia globose, echinulate; penicilli comparatively short; sterigmata somewhat divergent; pigmentation seldom diffusing throughout the surrounding agar. *P. aculeatum* Raper and Fennell 639

2′. Colonies developing red-orange, yellow-orange or greenish brown rather than deep red colors in reverse; surface usually characterized by prominent areas of sterile yellow aerial mycelium ..... *P. variabile* Sopp 642

b. Colonies on Czapek and steep agars very restricted or thin, never developing an intense red pigmentation; reverse variously colored in yellow to orange-brown, or greenish shades, sometimes more or less mottled ..... *P. rugulosum* series 646

Page

1′. Colonies restricted, close-textured, usually strongly folded or wrinkled.

aa. Conidia elliptical, conspicuously rugulose; penicilli typically biverticillate-symmetrical but often irregular in pattern ..... *P. rugulosum* Thom 648

bb. Conidia strongly elliptical, smooth or slightly and irregularly roughened; penicilli more consistently biverticillate-symmetrical ..... *P. variabile* Sopp (in the *P. purpurogenum* series)

2′. Colonies very restricted, or very thin and plane but with central area commonly raised or floccose.

aa. Colonies very thin throughout or with central area somewhat floccose, growing more or less restrictedly upon all substrata ..... *P. tardum* Thom 651

bb. Colonies growing very restrictedly upon Czapek, but heavily sporing and broadly spreading on media containing ammonium nitrogen ..... *P. diversum* Raper and Fennell 653

1″. Colonies producing abundant yellow, much branched mycelia on malt, often tending to characterize the culture... *P. diversum* var. *aureum* Raper and Fennell 655

3. Colonies with surface appearing almost lanose, loose-textured, comparatively deep; vegetative mycelium typically in yellow-green shades; conidiophores long and coarse, usually roughened; reverse deep to dark yellow-green, brown, or almost black, but seldom developing true reds ..... *P. herquei* series 658

a. Sclerotia lacking or rarely produced and limited in number; metulae numerous and somewhat divaricate; conidia elliptical.

1′. Conidiophores usually less than 1 mm. in length and 4.0 to 4.5μ in diameter ..... *P. herquei* Bainier and Sartory 659

2′. Conidiophores commonly 1 mm. or more, and up to 2 mm., in length by about 8μ in diameter.. *P. olsoni* Bainier and Sartory 664

b. Sclerotia very abundant, characterizing the species; metulae 3 to 5 in number, in compact verticils; conidia globose. *P. novae-zeelandiae* van Beyma 665

Penicillium luteum Series

Outstanding Characters

Perithecia characteristically produced, mostly in bright yellow to golden yellow or orange-yellow shades, soft, with growth indeterminate, individually consisting of fertile tissue bearing abundant asci bounded by a thin covering of interlacing hyphae which may range from very loose to closely knit but shows little or no cellular modification, typically surrounded by a loose mantle of coarse, encrusted, and richly pigmented hyphae.

Asci borne in chains, or singly as branches from ascogenous hyphae, 8-spored; ascospores variable, usually elliptical and showing no evidence

of equatorial markings, commonly spinulose over their entire surface but in certain species pitted or distinctively banded; in occasional members lenticular showing a prominent equatorial zone.

Colonies spreading broadly in some species, in others growing more restrictedly; usually close-textured on Czapek's agar and often developing perithecia late and in limited numbers only; growing more luxuriantly on malt agar and typically developing abundant perithecia which impart to these molds their characteristic yellow coloration, approximating *luteus* of Saccardo.

Penicilli abundantly produced in some strains, not in others; typically biverticillate and symmetrical but with monoverticillate or fractional structures often predominating in individual species and strains.

Sterigmata typically lanceolate or acuminate, *i.e.*, comparatively long and tapered in the manner characteristic of the Biverticillata-Symmetrica section. Conidia typically but not uniformly elliptical, with ends usually pointed and walls smooth; mostly in pale blue-green to gray-green shades.

Series Key

(See General Key to Biverticillata-Symmetrica)

This series includes some of the most colorful and most interesting members of the genus *Penicillium*. All are characterized by the production of perithecia, usually in abundance, which are surrounded by loose mantles or wefts of coarse, encrusted hyphae. In the majority of forms, this enveloping mycelium is highly pigmented in yellow to golden or orange-yellow shades and it is this aerial growth which imparts to the colonies their characteristic coloration.

Penicilli may be regarded as typically biverticillately-symmetrical, although many members seldom develop structures of this typical pattern. Simple monoverticillate structures predominate in some strains and species, asymmetric structures of varying complexity are most common in others, but in most species the penicilli are symmetrical and biverticillate, hence wholly typical of the section to which the series is assigned. Irrespective of the complexity of the conidial apparatus developed, the ultimate conidium bearing cells, or sterigmata (except in *Penicillium avellaneum* and *P. striatum*), are consistently lanceolate or acuminate and thus afford a reliable index of relationship.

The perithecia differ markedly from those of the *Penicillium javanicum* and the *Carpenteles* series already considered (see p. 132 and p. 260). Unlike the above, which are characterized by definite peridia composed of one to many layers of compacted thick-walled cells, the perithecia of the *P. luteum* series typically show no definite walls and are bounded only by net-

works of interlacing hyphae that remain essentially unmodified. In some species, such as *P. spiculisporum* Lehman, *P. bacillosporum* Swift, and *P. duponti* Griffon and Maublanc emend. Emerson, this covering may be rather closely knit and at times simulate a true perithecial wall, while in other species, such as *P. wortmanni* Klöcker and *P. luteum* Zukal, it may be very thin and hardly apparent. The perithecium seems to arise in a number of different ways among the several species that comprise the series (see below), but in all cases the course of development and the ultimate structure of the mature body appears to be approximately the same. Perithecial initials give rise to an enlarging mass of ascogenous elements which becomes enmeshed in, and is surrounded by a supporting and protective network of sterile and possibly nutritive hyphae. In most species the asci begin to appear quite early, often within 4 to 6 days. According to Emmons (1935), the fertile region may subsequently increase in size materially as a result of continued peripheral growth. On the other hand it may arise from more than one center of origin. In no case is a firm, brittle, or sclerotioid structure produced.

Asci are abundantly produced in most forms, and may be borne either in short chains or singly as lateral buds from successive cellular elements of the fertile hyphae. Emmons attached considerable importance to this difference, a view with which we concur. It is believed significant that in our key to the series (see p. 561), which is based upon other primary characters, the species that produce asci in chains fall into one general subseries, while those that produce asci singly as lateral buds fall into another sub-series.

Ascospore patterns and markings differ substantially within the series, and the differences exhibited are believed to provide a clue to natural relationships, since cultural characteristics and certain other details of structure can generally be correlated with them.

To be consistent with our general practice of adopting for a series the name of the species most representative of it, or the species most commonly encountered, we should refer to this as either the *Penicillium wortmanni* or the *P. vermiculatum* series rather than as the *P. luteum* series. However, this practice is not followed in the present case for the following reasons: (1) the name *P. luteum* is the oldest name applied to an ascosporic member of this section of the genus; (2) the name *P. luteum* is beautifully descriptive of the cultural aspect of the yellow ascosporic phase of most of the species comprising the series, and (3) the name has been widely adopted in the literature to include yellow pigmented Penicillia producing perithecia and ascospores.

The *Penicillium luteum* series, as presented here, is believed to represent a true natural series despite marked differences in ascospore patterns and

dimensions, in origin and arrangement of asci, in the form and complexity of perithecial initials, and in the overall coloration of growing colonies. Such differences are regarded as being outweighed by essential similarities existing between the perithecia produced and in the character of conidial structures, especially the sterigmatic cells. It is not possible in all cases to establish with certainty the correct inter-relationship of the species that comprise the *P. luteum* series, and a number of divergent lines of development are clearly apparent. These are discussed below.

Penicillium duponti was originally described by Griffon and Maublanc (1911) as a conidial species only. Thom (1930) placed it in his Asymmetrica-Velutina adjacent to *P. oxalicum* largely upon the pattern of its penicilli and the elliptical character of its conidia. He called attention to its thermophilic character. Recently, Professor Ralph Emerson has isolated from retting guayule shrub (45–47°C.) at Salinas, California, strains which duplicate almost exactly Griffon and Maublanc's description, but in addition produce soft perithecia of the general pattern developed in the *P. luteum* series. Furthermore, careful re-examination of the conidial apparatus shows this to be often irregular and asymmetric but typically biverticillate and sometimes symmetrical, and to bear lanceolate or acuminate sterigmata that are likewise typical of the *P. luteum* series. The species is, therefore, placed adjacent to *P. stipitatum* largely upon the common character of ascospores with equatorial furrows and ridges. Perithecial initials have not been observed in *P. duponti*.

Penicillium stipitatum Thom, as described by Emmons (1935) and as observed in our own cultures, produces ascospores and perithecial initials of unique pattern. The ascospores are lenticular rather than elliptical and show two prominent equatorial bands, often so closely appressed as to appear as a single ridge (fig. 147D). The presence of a definite equatorial zone with prominent ridges is strongly suggestive of the ascospores seen in some members of the *P. javanicum* and *Carpenteles* series. Reasonably close relationship to these series might be suspected were it not for other structural and cultural differences, and for the fact that the same type of ascospore is regularly seen in ascosporic species of *Aspergillus*. The structure of its perithecia, the pattern of its conidial apparatus, and the coloration of colonies upon many substrata unmistakably ally *P. stipitatum* with the *P. luteum* series. Perithecial initials are likewise unique as described and illustrated by Emmons (1935). In no other species have we observed a basal coil from which develops an elongate hypha that proliferates at its terminus to give rise to a perithecium (fig. 144A). Asci are produced in chains, a character that is shared by the majority of species assigned to the *P. luteum* series.

Penicillium vermiculatum Dangeard, *P. wortmanni* Klöcker, *P. helicum*

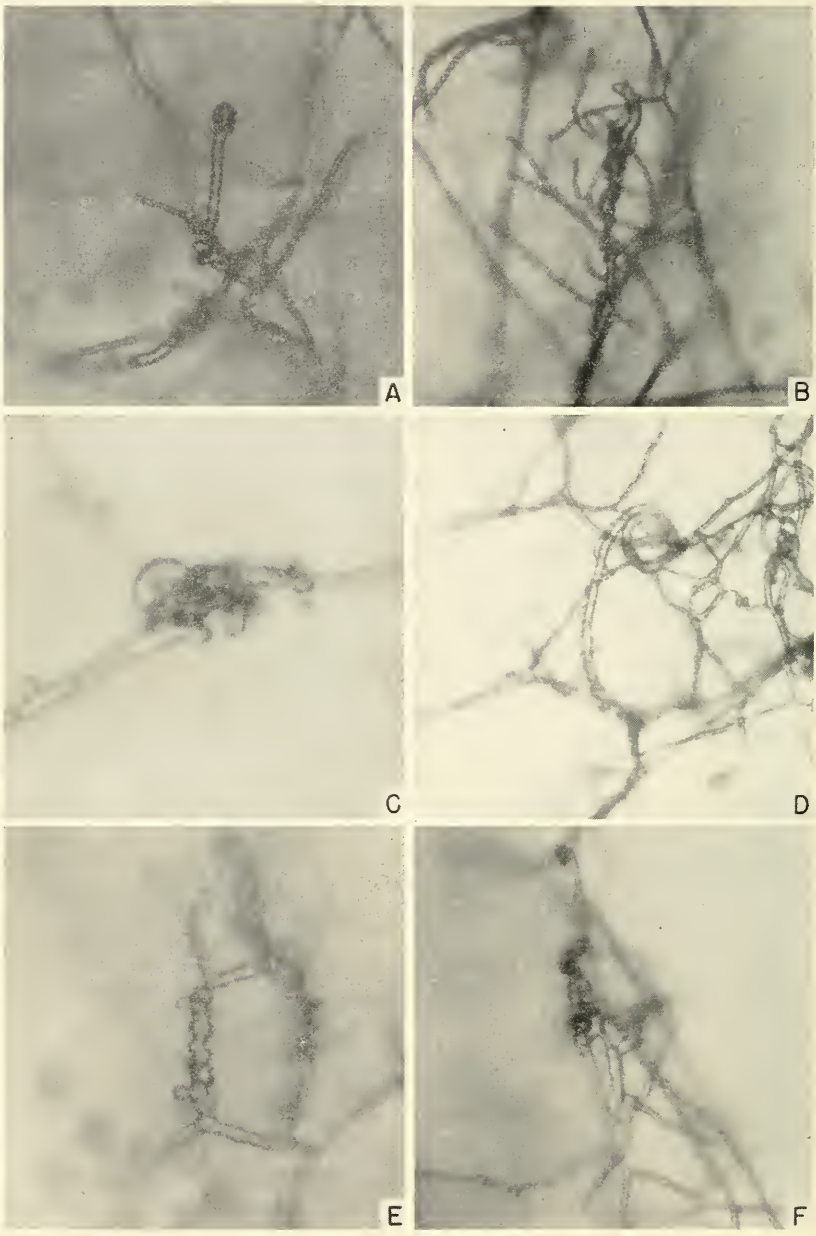


FIG. 144

Raper and Fennell and *P. rotundum* of the same authors are believed to be fairly closely related. All produce ascospores that are spinulose over their entire surface and show no sign of an equatorial zone. *Penicillium vermiculatum* is distinguished particularly by its long clavate to vermiform perithecial initials as reported and illustrated by Dangeard (1910), and subsequently verified by Emmons (1935). They are regarded as a distinguishing characteristic in the present study (fig. 144B). While it has not been possible for us to make cytological studies, superficial examination of typical strains suggests a strong possibility that this species produces true ascogonia and antheridia and that some type of sexual fusion may occur. Emmons (1935) believed an actual copulation took place but failed to observe such. *Penicillium wortmanni* in culture bears a striking resemblance to the above, and its ascospores are practically indistinguishable from those of *P. vermiculatum*. Perithecial initials, however, differ markedly. There is no indication of differentiation into ascogonia and antheridia, the first evidence of a developing perithecium being the appearance of swollen, deeply staining, intercalary segments of aerial hyphae which become broken up into short cells (fig. 144C) and may be more or less branched. In *P. rotundum* much the same condition prevails (fig. 144F), but the clusters of swollen cells are not limited to aerial vegetative hyphae and may even appear in structures that are penicillate and which apparently started out to develop as conidial structures. The production of globose spores clearly separates it from *P. wortmanni*. In *P. helicum* the perithecial initial first develops as a long, thickened, deeply staining hypha not markedly different from that of *P. vermiculatum*. A thinner hypha, possibly an antheridium, is almost invariably coiled around the base of the larger hypha probably representing an ascogonium, and terminates as a slightly flattened enlargement closely appressed against the wall of the latter. Cytological studies have not been made and we have not succeeded in determining whether any type of fusion occurs. In any case, at about

FIG. 144. Initial stages of perithecium, or ascocarp, formation in members of the *Penicillium luteum* series. *A*, *P. stipitatum* Thom, NRRL 2105; note the coiled hyphae at base, from which arises a heavy club-like structure that proliferates at its terminus to produce the young ascocarp, × 375. *B*, *P. vermiculatum* Dangeard, NRRL 2098; note the heavy clavate to vermiform hypha (presumably the ascogonium) around which a smaller hypha (possibly the antheridium) is tightly coiled, × 375. *C*, *P. wortmanni* Klöcker, NRRL 1017, first evidence of perithecial origin consists of irregular knots of enlarged hyphae as shown, giving no clue to identity of possible ascogonia and antheridia, × 800. *D*, *P. helicum* Raper and Fennell, NRRL 2106; a long thick non-septate hypha (ascognium?) first appears, which subsequently contracts into a spring-like coil—meanwhile a smaller hypha becomes tightly coiled around the basal portion of the large hypha, × 375. *E*, *P. spiculisporum* Lehman, NRRL 1026; initial stage appears as a heavy, irregular and usually knotted body as shown, × 800. *F*, *P. rotundum* Raper and Fennell, NRRL 2107; initials are most irregular in pattern and may even start as penicillate structures—the development shown is representative, but duplication of pattern need not be anticipated, × 675.

this time the long clavate hypha begins to coil terminally in a definitely helical pattern, and it is this structure which specifically distinguishes the species (fig. 144D). Ascospores, although elliptical and spinulose in character, are definitely smaller than those produced by *P. vermiculatum* and thus serve to further differentiate the species.

Penicillium spiculisporum Lehman should possibly be considered with the above. Ascospores are of the same general pattern as seen in *P. vermiculatum* and *P. wortmanni* and are intermediate in size between these species and *P. helicum*. Culturally the species is distinct, since it usually produces little or no yellow pigmentation in the coarse mycelia that surround the perithecia. In contrast to most members of the series, the perithecia of this species are at first white and in age seldom develop darker shades than cream or a light buff, although in his description, Lehman (1920) noted the development of pink tints upon some substrata. The hyphal networks that bound the perithecia are commonly denser than in most species and often simulate a true wall, but in our experience never develop a specialized membrane of differentiated cells. The perithecial initials are somewhat suggestive of those seen in *P. wortmanni* but are usually less diffuse and often appear as a single, irregularly swollen deeply staining cell that branches profusely (fig. 144E) to produce a knot of fertile tissue which subsequently develops into the perithecium.

Penicillium bacillosporum Swift, like *P. rotundum*, produces globose, spinulose ascospores, but shows little additional evidence of possible close relationship to the latter species. Perithecial initials are in the form of two short coiled hyphae and are strikingly similar to those produced in *P. luteum* Zukal (Emmons, 1935). Mature perithecia show the basic pattern and structure characteristic of the group but are commonly bounded by a more closely knit network of interlacing hyphae than in most other species. The penicilli, while commonly monoverticillate, may be regarded as conforming with the basic pattern of the series since the sterigmata are typically lanceolate and since occasional biverticillately-symmetrical structures are observed. The conidia, however, are quite unlike those of any other *Penicillium*. These are bacilliform, rod-like, and this character clearly differentiates it from all other known species (fig. 153). Pigmentation differs from most members of the series; colonies regularly show lighter yellow shades, with vegetative hyphae showing reddish or greenish tints, and develop colony reverse in various dark brown to green shades rather than reddish or reddish browns. Asci are borne in short chains as in all of the above species. While close relationship is not presumed, this species is perhaps closer to *P. spiculisporum* than to any other member of the series as shown by the usual absence of bright yellow colors in the

mycelium; more closely interlaced hyphal networks surrounding its perithecia; and the common occurrence of monoverticillate penicilli.

Penicillium luteum Zukal is the oldest of the recognized members of the series and is at the same time one of the least well known species. This results from the infrequent isolation of Zukal's form, and from the confusion attendant to the assignment of various other ascosporic forms to this species by later investigators. Our diagnosis of the species is based upon the strain used by Emmons (1935) in his study of ascocarps in *Penicillium*, and we have every reason to believe that it is representative of Zukal's original isolate. The perithecia are unusually loose-textured, as in *P. wortmanni*, and are accompanied by the development of abundant encrusted hyphae of bright yellow color which give to the culture upon most substrata a coloration that is truly "luteus." Penicilli are often fractional but are otherwise wholly characteristic of the series. Perithecial initials are in the form of two short coiled hyphae as reported and illustrated by Emmons (1935). Ascospores are unique and diagnostic of the species, and may be characterized as follows: broadly elliptical, with walls smooth or nearly so except for a spiral band or bands of raised protuberances or echinulations which, under the microscope and in any single plane, appear transverse (or tricostate, *fide* Zukal). Asci are not borne in chains as in all of the above species, but develop as lateral buds from fertile hyphae as in members of the *P. javanicum* and some members of the *Carpenteles* series. A degree of relationship to these forms may thus be indicated.

Penicillium avellaneum Thom and Turesson is usually separated from other members of the series upon the basis of its tan to light brown (avellaneous) conidia. In addition to this character the conidial apparatus itself is somewhat unique. Although often appearing symmetrically biverticillate it typically consists of a larger number of crowded metulae, and withal produces an unusually large and compact penicillus (fig. 143C). Metulae are generally heavier than in most species and the sterigmata usually fail to show the characteristic lanceolate pattern of the Biverticillata-Symmetrica section. Despite these differences, the species is regarded as properly assigned here. Perithecia are regularly accompanied by the production of mantles of coarse, encrusted, yellow hyphae and show the basic structure characteristic of other members of the series. Usually accompanying the development of perithecia, and sometimes in their absence, are coarse hyphae with walls in purple or purple-red shades which when massed lend to the colony a marked purple pigmentation in surface and reverse. Thom and Turesson (1915) figured the perithecium as bounded by a single layer of specialized, flattened, and thick-walled cells. Careful examination of different strains in the present study has failed to show such

a peridium of specially differentiated cells. As in other members of the series, the perithecium appears to be bounded by a network of interlacing hyphae. The pattern of the perithecial initials has not been established since these structures regularly develop in areas of comparatively dense growth well within the margin of established colonies. Asci are borne as lateral buds from fertile hyphae as in *P. luteum* and *P. striatum*. Ascospores are large, elliptical, show no evidence of an equatorial furrow, and are delicately pitted over their entire surface.

Penicillium striatum Raper and Fennell is doubtfully a member of the *P. luteum* series, but can be keyed here more satisfactorily than elsewhere. Certain of its characteristics indicate a considerable measure of true relationship. This is suggested particularly by the character and texture of its perithecia, which strongly resemble those of *P. luteum* and *P. wortmanni* except for a lack of yellow pigmentation in the coarse enveloping hyphae. Asci are borne as lateral buds from ascogenous hyphae (fig. 157E) and in size, shape, and mode of origin bear a striking resemblance to *P. avellaneum* considered above. The ascospores are unique in the pattern and degree of their markings. They are broadly elliptical, and smooth-walled except for a series of thin, comparatively wide, wavy, longitudinal ridges or frills (fig. 157F) which tend to converge at opposite ends of the spore. There is no suggestion of an equatorial band. Penicilli are comparatively scarce and inconsistent in pattern, hence offer little help as a possible clue to relationship. Symmetrically-biverticillate structures have not been observed, nor are the sterigmata lanceolate-acuminate in the manner typical of the Biverticillata-Symmetrica. At the same time they are not sufficiently characteristic of any other group in the genus *Penicillium* to suggest more accurate placement elsewhere. Continued examination of newly isolated ascosporic Penicillia may in time reveal transitional species or otherwise provide a satisfactory basis for correct placement of this species. Until that time, we believe it is best to retain it here where it can be found with other forms which at least produce an ascosporic phase possessing certain similarities.

Members of the *Penicillium luteum* series as it is here constituted are by definition, typically ascosporic. Individual strains belonging to different member-species, however, commonly lose their capacity to produce perithecia and ascospores, and subsequently may be perpetuated in laboratory culture without the reappearance of this developmental phase. While it is possible that these represent unisexual haplonts, and that by proper pairing of such asexual strains the capacity to produce perithecia might be restored, such attempts have been consistently unsuccessful in our experience. Emmons (1935) reported all of the species studied by him, including *P. wortmanni* Klöcker, *P. vermiculatum* Dangeard, *P. spiculi-*

sporum Lehman, *P. bacillosporum* Swift, *P. stipitatum* Thom, and *P. luteum* Zukal to be homothallic. Prior to this, and working with a different strain of *P. luteum*, Derx (1925, 1926) had reported this species to be heterothallic and presented tabular evidence of paired monospore cultures in support of his view. Emmons accepted Derx's results as evidence of cultural variation within his stock strain rather than as proof of heterothallism. Irrespective of their origin, which is a matter that requires much additional careful study, these sterile variants commonly develop in culture and being of known lineage, are retained in the *P. luteum* series. This immediately raises the question of the proper assignment of newly isolated strains which show considerable evidence of relationship to the above but never show any evidence of sexuality. In his Monograph, Thom (1930) referred to these as belonging to the "*P. luteum* series, nonascosporic." The accuracy of such an assignment probably cannot be improved upon. However, we believe it less confusing taxonomically to consider such forms solely upon the basis of their conidial structures and colony characteristics, and such a course is followed in the present work. They are assigned to such predominately yellow-green species as *P. variabile* and *P. verruculosum* in the *P. purpurogenum* and *P. funiculosum* series, respectively.

Many investigators have noted similarities between the perithecia of *Penicillium luteum* and those of the genus *Gymnoascus*. As early as 1895 Saccardo (Sylloge *XI:* 437–438) transferred Zukal's species to *Gymnoascus* upon bibliographic considerations. Thom (1930) considered this placement, but concluded that many other characters indicating relationship with true Penicillia outweighed it, and kept the species in *Penicillium* where Zukal had originally placed it. Dodge (1933) and Emmons (1935) likewise recognized close similarities between certain members of the series, particularly *P. wortmanni*, and *Gymnoascus* but like Thom left them in *Penicillium*. Continued study of the forms now in our possession, together with the examination of additional isolates, may in time enable us to clarify the true relationship of these two genera. For the present, however, we believe that the user of this Manual will benefit if we consider together in one genus all of the molds which produce true penicillate conidial structures, irrespective of the structure of their perithecia.

Penicillium duponti Griffon and Maublanc emend. Emerson, published here.
P. duponti Griffon and Maublanc, in Bul. Soc. Myc. France **27:** 68–74, figs. 4–8. 1911, represented the conidial stage only.

This species is unique among the Penicillia in being strongly thermophilic, growing at temperatures between 25° and 60°C., with an optimum at 45° to 50°C. The species is known only from the original description based upon two isolates, and from additional strains isolated by Professor Ralph

Emerson in 1945 from retting guayule shrub at Salinas, California. Because of its role in the retting process, Emerson has studied the species quite exhaustively and has discovered an ascosporic stage which was unreported by the describers.

Penicillium duponti is assigned to the *P. luteum* series upon the bases of its biverticillate penicilli with conspicuously lanceolate sterigmata bearing strongly elliptical conidia and its perithecia with soft plectenchymatous walls.

The following emended description is based primarily upon notes furnished by Emerson, supplemented to a limited degree by our own observations of his strain No. 26 (now maintained as NRRL 2155):

Colonies on glucose-yeast agar growing rapidly at optimum temperatures of 47° to 50°C., attaining a diameter of 7.0 to 8.0 cm. in 7 to 10 days; delicately floccose, becoming somewhat mealy in older cultures, usually 1 mm. or less deep, in age developing deeper tufts as overgrowths; variable in color depending upon temperature, age, and other factors, at first white and later developing dull shades of grayish green, lavender, or pinkish brown; exudate irregularly produced, dark brown in color; reverse and agar pinkish lavender or reddish brown. Mycelium branched, delicate, mostly 2.0 to 2.5 or 3.0μ in diameter. Conidiophores short, usually arising more or less perpendicularly as lateral branches from the main hyphae, often simple but not infrequently with 2, 3, or 4 irregular branches, septate, 5 to 30μ in length by 2 to 3μ diameter, slightly larger at the apex than at the base, smooth-walled. Penicilli irregular (figs. 145A and B), varying from monoverticillate with 1 to 4 sterigmata at the apex of a short conidiophore, to partially biverticillate, or fairly regularly biverticillate; metulae few in the verticil, 5 to 7μ by 2 to 3μ; sterigmata acuminate, divergent, 8 to 10μ by 2μ. Conidia in long tangled chains, readily separating from the sterigmata without disjunctors, pale yellowish when mature, smooth, elliptical to ovoid, 2 to 4.5μ by 1.5 to 3.0μ (fig. 145A).

Perithecia not produced upon glucose-yeast agar but occurring regularly and abundantly on moist, chopped guayule shrub in pure-culture rets and occasionally on oatmeal agar cultures, at first white and cottony, 4 to 5 days at 45°C., then (7 days) pearl gray, soft, pliable and delicately leathery, with an external surface of fine interwoven hyphae; finally (14 days) pale grayish tan, up to 1 mm. or more in diameter (figs. 146A and B), with a brittle or papery peridium which fractures fairly cleanly under pressure, scattered or irregularly clustered but usually not confluent, subglobose, 0.4 to 1.3 mm. diameter; peridium indehiscent, plectenchymatous (fig. 146C), the outer elements very small and compact, the inner becoming larger (up to 10μ diameter), less compact, and forming an almost pseudoparenchymatous tissue; asci very numerous, scattered, subglobose, 9–10μ diameter, 8-spored, disintegrating before the spores mature (fig. 145C);

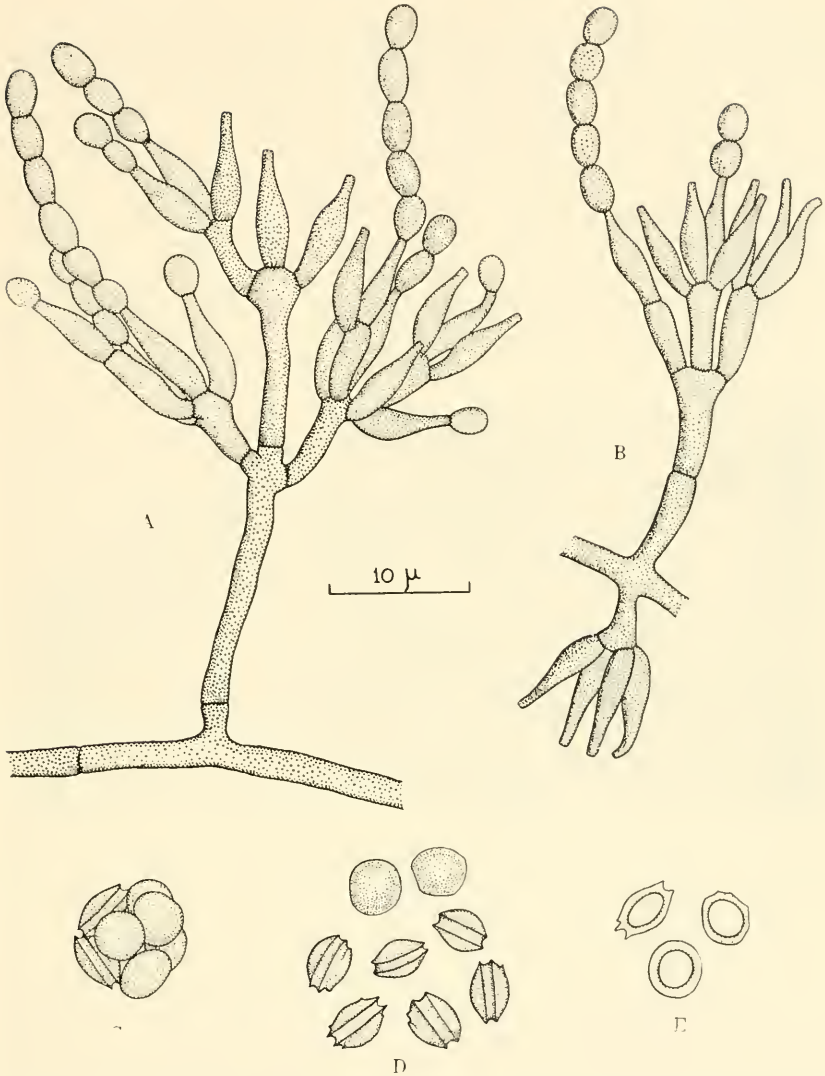


FIG. 145. *Penicillium duponti* Gr. and Maub. emend. Emerson. *A* and *B*, penicilli, indicating the irregularities encountered. *C*, Ascospores remaining in original positions after early disappearance of ascus wall. *D*, Mature ascospores in surface view showing characteristic equatorial furrow and ridges. *E*, Ascospores in optical section. (Camera lucida drawings by Ralph Emerson.)

ascospores generally lenticular, 3.5–5.0μ by 2.5–3.5μ, usually with a quite well defined equatorial furrow flanked by low, smooth, or somewhat jagged ridges, with convex surfaces smooth or showing occasional ridges and ir-

regularities (fig. 145D and E), distinctively pale orange or tan in mass, very pale yellow when viewed singly. Spores mature in 10 to 14 days at 45°C., and will germinate without special treatment within 24 hours at 45°C., the two valves of the wall separating.

Colonies on Czapek solution agar growing less rapidly, very thin, flocculent, attaining a diameter of 4.0 to 5.0 cm. in 10 to 12 days at 45°C., remaining white longer, but at length becoming pale lavender, cinnamon pink, or avellaneous but usually not showing grayish green shades from developing conidia.

Colonies on steep agar closely approximate those on glucose-yeast agar in rate of growth, texture, color, and in the abundance of conidium production.

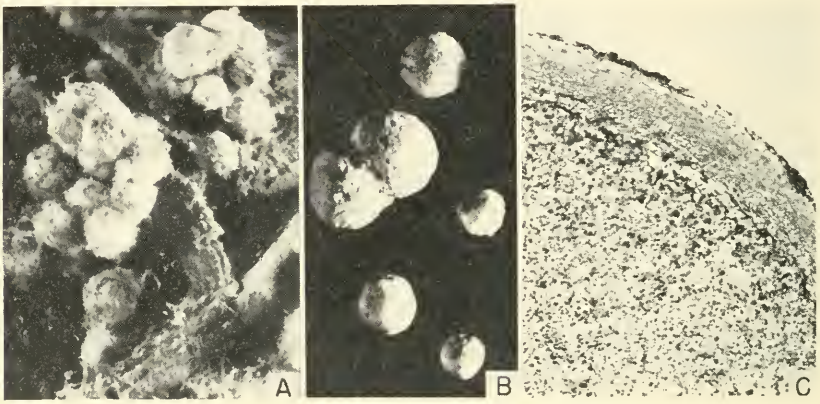


FIG. 146. *Penicillium duponti* Gr. and Maub. emend. Emerson. *A*, Nearly mature perithecia on chopped guayule shrub incubated 14 days at 45°C., × 9. *B*, Mature perithecia dissected out, × 9. *C*, Cross section of nearly mature perithecium showing plectenchymatous peridium and fertile cavity filled with asci and ascospores, × 150. (Photographs by Louis C. Erickson for Ralph Emerson.)

On chopped guayule shrub, growth is at first white, delicate, cottony, then becoming pale gray to yellowish green with the start of conidium-formation, and in age dark mouse gray with a greenish cast. White knots of hyphae begin to be very conspicuous in 4 or 5 days at optimum temperatures and subsequently develop into the pale gray perithecia that characterize the species (fig. 146).

A similar but generally somewhat delayed development of conidial structures and perithecia occurs in deep cultures of sterilized cracked or rolled oats.

Species isolated originally by Griffon and Maublanc from fresh manure which "heated naturally" and from wet hay in an incubator at 50°C. Subsequently isolated by Emerson as follows: "Origin: Self-heated, retting

guayule shrub, removed and incubated at 45°C., May 1945; also guayule shrub retted at controlled temperatures of 47°C. in continuously rotating drum and subsequently removed and incubated at 47°C., December 1945."

Emerson writes as follows regarding the species:

"*Penicillium duponti*, like all the molds isolated from retting guayule, actively decomposed guayule resins in resin-emulsion media; and, in pure culture rets, lowered the resinous fraction of the crude rubber from 18 per cent to 11 per cent.

"Until the present isolate was obtained from guayule, *Penicillium duponti* had apparently not been seen since its discovery by Griffon and Maublanc in 1911. Their careful description fits the present strains with remarkable closeness. The species still occupies a unique position, recognized by Griffon and Maublanc, as the only true *Penicillium* which can be justly included in the small group of molds known to be strongly thermophilic.

"By germinating the ascospores and obtaining therefrom the typical conidial stage of *Penicillium duponti*, the genetic relation between the sexual and asexual phases was definitely established. The tests necessary to determine whether the species is homo- or hetero-thallic have not yet been made. Nor are the factors understood which stimulate the formation of perithecia. The particular prevalence of perithecia in the lower layers of shrub in pure culture rets suggests that partial deficiency of oxygen may play a role. This idea has been borne out to some extent in experiments where perithecia were abundantly produced in agar cultures held under reduced oxygen pressures, but carefully controlled studies will be required to clear the matter up."

Perithecia in *Penicillium duponti*, as described and photographed by Emerson (fig. 146), commonly show a heavier peridium than other members of the *P. luteum* series. These, however, differ mostly in thickness rather than in basic structure. In *P. stipitatum*, the species next to be considered, perithecial walls of closely interwoven hyphae approaching those of *P. duponti* are often seen.

Penicillium stipitatum Thom, Emmons, Mycologia **27:** 138–141, figs. 6, 7, and 16. 1935.

Emmons' description as follows:

"Colonies on Czapek's solution agar floccose, tufted in yellow (*luteus*) shades passing over to orange or even red-orange shades in age; reverse yellow to red-orange; aerial hyphae studded with granules yellow in the young and growing period becoming reddish in age; conidial apparatus irregularly biverticillate with sterigmata up to 10 by 2μ, taper pointed and closely packed in the verticil; conidia about 3.5μ in long axis, rather thick-walled fusiform smooth; ascogenous masses enveloped by tufts and masses of yellow hyphae, within which hyphae are arranged into a fairly definite wall forming a brittle and easily crushed perithecium; asci 8-spored, ripening quickly, 5.5–6.5 x 7–8μ.

"Ascospores 3–3.6μ in long axis by about 2μ, lens-shaped consisting of a two valved body with an equatorial band or frill about 0.5μ in width, usually appearing singly but occasionally apparently double with a groove partially evident between them."

Our notes augmenting Emmons' description follow:

Colonies on Czapek's solution agar growing fairly rapidly, attaining a diameter of 3.5 to 4.0 cm. in 2 weeks (fig. 147A), consisting of a floccose, tufted felt about 0.5 to 1.0 mm. deep in central area, comparatively tough,

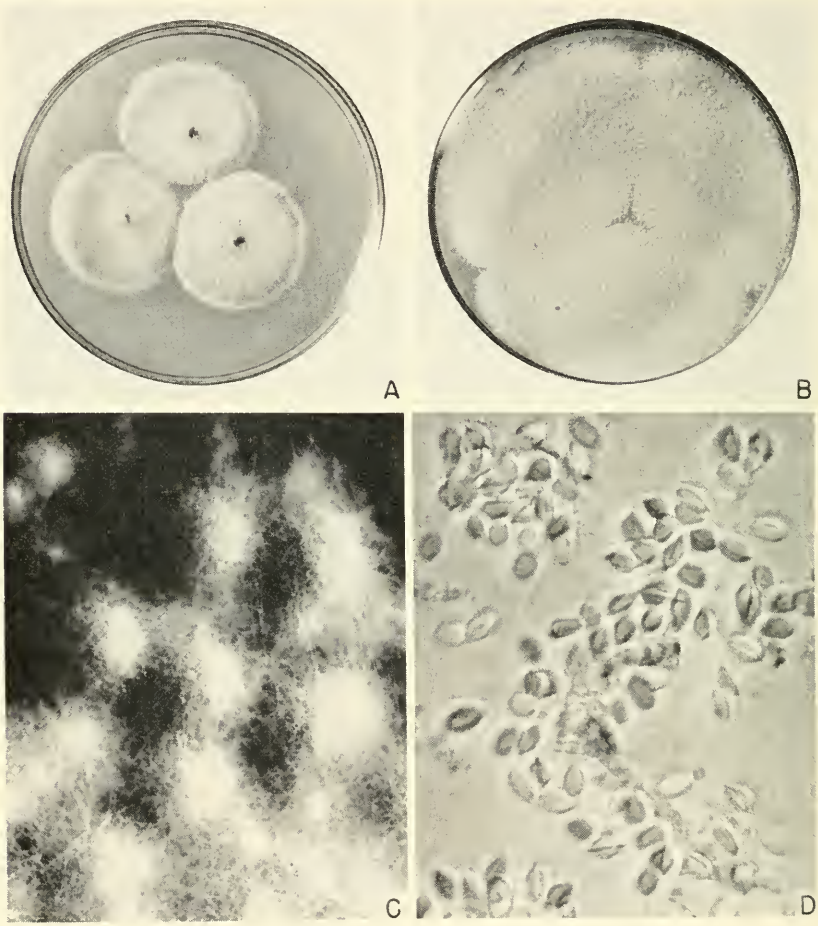


FIG. 147. *Penieillium stipitatum* Thom. *A* and *B*, Ten-day-old colonies of NRRL 1006 on Czapek and malt agars. *C*, Perithecia in NRRL 2105 as seen under low powers, × 30. *D*, Mature ascospores, × 1500; note the conspicuous equatorial ridge that is characteristic of this species.

producing abundant perithecia in a layer near or adjacent to the agar surface, commonly obscured by an overlying mycelial felt, azonate, at first in bright yellow shades near citrine yellow, in our cultures developing a greenish cast in age; penicilli lacking or limited in number, usually frac-

tional (more abundant on hay, cornmeal, and 20 percent-sucrose-Czapek agars); exudate lacking or limited; odor pronounced, suggesting mushrooms; reverse in yellow to orange-brown shades with pigment diffusing throughout the surrounding agar; penicilli varying in form and complexity from comparatively simple (fig. 143A) through irregular patterns to occasionally almost biverticillately-symmetrical, borne on very short conidiophores arising mostly from the substratum; metulae, when present, variable but commonly about 10μ by 2.5μ; sterigmatic cells tapered in the manner characteristic of the group, variable, from 10 to 12μ by 2.0 to 2.5μ; conidia elliptical to ovate or pyriform, variable in size, mostly 3 to 4μ in long axis by 2.0 to 2.5μ, occasionally up to 6 or 7μ by 3.0 to 4.0μ, smooth-walled; perithecia round or nearly so, variable in size up to 300μ in diameter with fairly definite wall composed of compacted hyphae a few cell layers in thickness, usually surrounded by a loose mantle of thick, encrusted, uncoiled and little branched hyphae (fig. 147C); asci produced abundantly throughout the perithecium upon an interlacing network of fertile hyphae, in short chains, subspherical to elongate when mature, about 6.5 to 7.5μ in long axis, 8-spored; ascospores as originally described (fig. 147D).

Colonies on malt agar spreading broadly, up to 7.0 to 8.0 cm. in 2 weeks, plane (fig. 147B), with vegetative mycelium largely submerged, producing abundant perithecia in a dense layer at the agar surface, often overgrown and partially obscured by a loose, ephemeral network of aerial hyphae, azonate, yellow in color near amber to citron yellow (Ridgway, Pl. XVI); perithecia as described above; penicilli lacking or sparingly produced.

Colonies on cornmeal agar spreading broadly, 7 to 8 cm. in 10 to 12 days, very thin, with vegetative mycelium largely submerged, producing scattered perithecia and conidial structures throughout the entire colony; perithecia as above but seldom more than 200μ in diameter; penicilli as described above.

Perithecial initials (fig. 144A) easily observed in young colonies upon malt and cornmeal agars. Concerning these structures and the development of perithecia, Emmons reported as follows in 1935 (p. 139):

"In *Penicillium stipitatum* two similar or barely differentiated hyphae arise as side branches, usually from different hyphae, and coil around each other (fig. 7A). After about two turns they fuse by a large pore so that the opening is of a diameter equal to that of the inside of the hypha. This opening is permanent. The two branches that initiate this development are without doubt the ascogonium and the antheridium. From our knowledge of what takes place in other fungi we may assume that fertilization takes place at this point. Cytological proof in this case has not yet been obtained. We would now expect the development of an ascocarp around this structure as in other Penicillia. The actual development is quite different. One of the branches, or the hypha arising from the union of the copulating branches, elongates until it reaches a length of 100–150μ (fig. 7A). It becomes once or twice

septate, and at its tip begins to put out branches. These gnarled branches are formed in profusion, become septate, and by their further branching and interwining, form a more or less compact mass not unlike the ascocarpic initial of *P. spiculisporum*. Within this ascocarp ascogenous hyphae appear and give rise to asci arranged end to end in chains (fig. 7B)."

The species description as presented above is based upon Emmons' original diagnosis and our observations upon one of his type strains, isolated in 1931 from rotting wood in Louisiana and now maintained as NRRL 1006. Two new isolates have been examined, namely: NRRL 2105 isolated in June 1946 from a sample of Minnesota soil, and NRRL 2104 isolated in January 1946 from a sample of soil from Sweden. The three cultures are alike in all particulars.

Penicillium stipitatum Thom is distinguished from other members of the *P. luteum* series primarily by the unique patterns of its perithecial initials (as described above) and its ascospores. In only one other member of this series, *P. duponti*, have ascospores with equatorial ridges been observed and these are not closely appressed as in *P. stipitatum*. As pointed out by Emmons, the equatorial band in ripening spores is oriented parallel with the wall of the enveloping ascus. When subsequently freed of the ascus, the equatorial ridges commonly show the curved pattern assumed during this development.

Penicillium vermiculatum Dangeard, in Le Botaniste **10:** 123–139, Pls. 16–20. 1907. See also Emmons, Mycologia **27:** 136–137, figs. 4 and 5. 1935; and Thom, The Penicillia, pp. 450–451. 1930.

Colonies on Czapek's solution agar attaining a diameter of 2.5 to 4.0 cm. in 2 weeks (fig. 148A), differing markedly in color and texture in different strains, sometimes predominantly yellow, near empire yellow to lemon chrome (Ridgway, Pl. IV) from abundant perithecia and enveloping pigmented hyphae, in other strains developing reddish colors with fewer perithecia and fairly abundant conidial structures in localized areas, in still other strains at first white or nearly so, soon becoming cream, tan, or flesh-colored, close-textured, fairly tough, with surface appearing almost floccose, and with conidial structures and perithecia lacking or very limited in number; exudate limited to abundant, clear, or lightly colored; odor fairly strong, suggesting mushrooms; reverse in yellow to light red shades; penicilli produced in varying numbers in different strains, ranging from fragmentary to typical biverticillately symmetrical (fig. 148C), borne primarily on erect conidiophores arising from the substratum; conidiophores mostly 300μ or less by about 3.0 to 3.5μ, smooth-walled; penicilli typically very compact, consisting of verticils of 4 to 6 metulae that measure about 8.0 to 10.0μ by 2.5 to 3.0μ and bear crowded clusters of 6 to 10 sterigmata

measuring about 7.0 to 8.0μ by 2.0 to 2.5μ, tapering to conspicuous conidium-bearing tips; conidia elliptical with ends often somewhat pointed, smooth-walled, about 2.5 to 3.0μ by 2.0 to 2.5μ, in occasional strains slightly larger or smaller; perithecia produced irregularly (see malt agar).

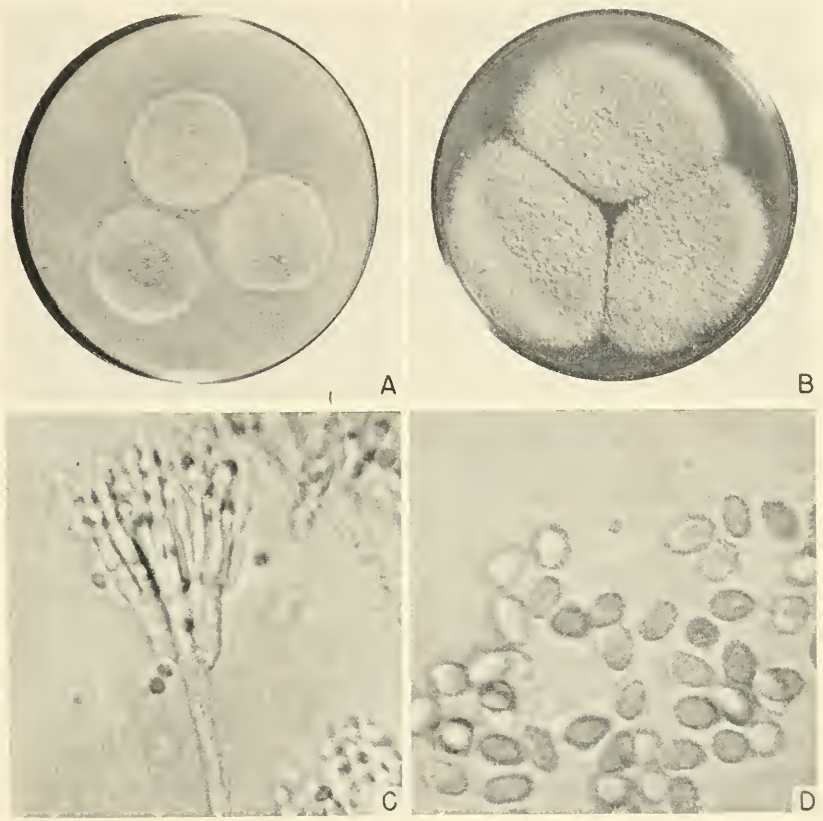


FIG. 148. *Penicillium vermiculatum* Dangeard. *A* and *B*, Ten-day-old colonies on Czapek and malt agars. *C*, Detail of a typical penicillus, × 1000. *D*, Mature ascospores, showing characteristic elliptical form and conspicuously echinulate walls, × 1500.

Colonies on malt agar (Col. Pl. IX), spreading broadly, up to 7.0 cm. in 10 to 12 days (fig. 148B), yellow to yellow-orange throughout (R., Pl. IV) in most strains from abundant perithecia and enveloping pigmented mycelia, in some strains showing reddish colors in age and in others developing abundant conidial heads in marginal to submarginal zones 1 to 2 cm. wide, in dull yellow-green shades near tea green (R., Pl. XLVII), conidial structures as described above except conidiophores up to 500μ in length and

metulae and sterigmata usually slightly longer and thinner than on Czapek; perithecia produced abundantly in all typical cultures, usually forming a continuous single layer near the colony margin and more or less piled in central areas, varying greatly in dimensions in different strains or even in the same strain, commonly 200 to 500μ in diameter, soft at all stages of development, with "walls" consisting of thin loose networks of pigmented vegetative hyphae, and surrounded by loose mantles of coarse, encrusted, and often twisted, radiating hyphae up to 200μ or more in length (fig. 15D); asci produced abundantly throughout the perithecium, borne in short chains, oval to almost globose at maturity, about 8 to 10μ in diameter, 8-spored; ascospores elliptical, conspicuously echinulate over the entire surface (fig. 148D), usually 4.0 to 4.5μ by 3.0 to 3.5μ, in some strains slightly longer, up to 5.0 or 5.2μ in long axis, slightly yellow.

Colonies on cornmeal agar spreading broadly, up to 7 cm. in 10 to 12 days, thin, typically consisting of a layer of scattered perithecia bright lemon yellow in color and few conidial heads not affecting the colony appearance; perithecia as described on malt.

Initials of perithecia (fig. 144B) are easily recognized on cornmeal agar and typically consist of long, thick, club-shaped hyphae (ascogonia) 100μ or more in length by 4.0 to 5.0μ in diameter (in contrast to vegetative hyphae about 2.0μ in diameter) around which thinner hyphae (antheridia?) characteristically coil.

Species description centered upon NRRL 1019 from K. D. Butler, University of Arizona, Tucson; NRRL 2100 isolated from soil from Sao Paulo, Brazil, in December 1945; and by numerous other strains that have been isolated from soils from Brazil, India, Nicaragua, Sweden, Egypt, and various parts of the United States. Typical strains have also been encountered among the molds isolated from exposed tentage in New Guinea and Panama. Two strains received in June 1946 from the Centraalbureau as *Penicillium luteum* Zukal, namely: NRRL 2098 from Neill in New Zealand (1938) and NRRL 2099 isolated at Baarn in 1936, are entirely typical of the species *P. vermiculatum*.

A total of 21 strains belonging to this species has been examined in the current study. Of these, 14 are regarded as entirely typical of the species and develop abundant characteristic perithecia and ascospores. Five produce conidial structures generally conforming with the above description and still show the characteristic club-shaped perithecial initials, but fail to produce perithecia upon any culture medium investigated.

One strain, NRRL 2101, from Professor Weston as an isolate from exposed cotton fabric in Panama, differs from typical strains by producing ascospores about 6.0 to 6.5μ by 2.0 to 4.5μ, bearing long, thin, colorless spines up to 1.0μ in length, and colonies with reverse in deep red to brown

PLATE IX

TOP: Penicillium vermiculatum Dangeard, NRRL 2098, on malt agar, 12 days. *CENTER: Penicillium rotundum* Raper and Fennell, NRRL 2107, on malt agar, 14 days. *BOTTOM: Penicillium avellaneum* Thom and Turesson, NRRL 1938, on malt agar, 12 days. (Color photographs by Haines, Northern Regional Research Laboratory. Reproduced through co-operation of Chas. Pfizer & Co., Inc.)

shades. The culture shows considerable strain individuality. Another strain shows ascospores intermediate between the above and typical cultures covered by the species description. As in many other species there seems to be considerable variation in the size of ascospores produced.

NRRL 1009, included among the strains which are no longer ascosporic, represents Thom's strain No. 11 which he reported as *Penicillium luteum* in 1910, after having received Wehmer's confirmation of his identification. In his Monograph (1930) Thom regarded *P. vermiculatum* Dangeard as synonymous with *P. wortmanni* Klöcker. Prior to this date, Derx (1925) had examined many ascosporic Penicillia including Thom's No. 11 and had reported this culture to represent Dangeard's *P. vermiculatum*. This disposition was not recognized by Thom (1930, pp. 448 and 451). Careful re-examination of NRRL 1009 convinces us of the correctness of Derx's assignment, for, although this strain no longer produces perithecia, its broadly spreading colonies are characteristic of *P. vermiculatum* rather than *P. wortmanni* and it still produces in large numbers the club-shaped ascogones which distinguish *P. vermiculatum*. Upon cornmeal agar it produces cellular masses which suggest young perithecia but, in our experience, has failed to produce ascospores. Also included among the non-ascosporic forms is NRRL 1011 received from Emmons in 1937 as his No. 228b and presumably one of the strains included in his study published two years earlier. This culture still produces abundant yellow mycelium in loose tufts which may be regarded as abortive perithecia. No asci or ascospores have been observed.

Cultures of *Penicillium vermiculatum* as isolated from nature regularly produce abundant ascospores. Such strains, however, commonly lose their capacity to develop fertile perithecia when maintained in artificial culture for considerable periods of time. Of the five cultures cited above as no longer ascosporic all have been under laboratory cultivation for 10 years or more.

Penicillium wortmanni Klöcker, in Compt. Rend. Lab. Carlsberg **6:** 100. 1903. See also, Biourge, Monogr., La Cellule **33:** fasc. 1, pp. 243–244. 1923; Thom, The Penicillia, pp. 449–450. 1930; and Emmons, Mycologia **27:** 133–135, fig. 1. 1935.

Colonies on Czapek's solution agar growing rather restrictedly (fig. 149A), about 2.0 to 3.0 cm. in 12 to 14 days at room temperature, varying markedly in color and texture depending upon the individual strain, commonly consisting of a tough mycelial felt with surface often appearing lightly floccose or fibrous, usually more or less zonate, with growing margin white, 1 to 2 mm. wide, and with central areas showing zones of either yellow mycelium or blue-green conidial heads, or both, in some strains

producing abundant conidia that characterize the colony and appear in yellow-green shades near tea green to pea green (Ridgway, Pl. XLVII), in others showing few or no conidial heads and usually becoming yellow-orange; exudate lacking or limited in amount, clear; odor suggestive of mushrooms; reverse in deep orange to tawny shades (R., Pl. XV); penicilli typically biverticillate and symmetrical (fig. 149C), borne on conidiophores arising primarily from the substratum, up to 200μ or more in length by 2.2 to 2.6μ, smooth-walled; metulae in compact verticils of 5 to 7 or 8, about 10 to 12μ by 2.0 to 2.5μ; sterigmata in very compact clusters, parallel, usually 5 to 8 in the verticil and measuring 10 to 12μ by 1.5 to 2.0μ, with the terminal portion characteristically tapered; conidia elliptical, with ends commonly more or less pointed, mostly 3.0 to 3.5μ by 1.8 to 2.2μ, in occasional strains slightly larger; perithecia produced in limited numbers in some strains, not in others (see malt agar).

Colonies on malt extract agar growing restrictedly but somewhat more rapidly than on Czapek (fig. 149B), about 3.0 to 4.5 cm. in 2 weeks, typically consisting of a heavy development of perithecia with or without an admixture of conidial structures, in some strains yellow-orange throughout from massed perithecia and enveloping pigmented hyphae, in others mixed yellow and yellow-green from the development of abundant conidial heads among the perithecia; conidial structures as described above; perithecia varying greatly in dimensions, commonly 100 to 300μ in diameter without definite walls and in crowded areas tending to merge and lose their identity, surrounded by loose mantles of heavily encrusted and strongly pigmented hyphae; asci abundantly produced throughout a loose hyphal network, borne in short chains, oval to sub-spherical, about 8 to 10μ in diameter, 8-spored; ascospores elliptical, spinulose over their entire surface (fig. 149D), mostly 4.0 to 4.5μ by 3.0 to 3.3μ, colorless or nearly so.

Colonies on cornmeal agar growing restrictedly, about 2.0 to 2.5 cm. in 2 weeks, thin, with vegetative mycelium largely submerged, conidial structures usually limited in number, generally not affecting the colony appearance, producing perithecia in an irregular layer heaviest at the colony center and thinning toward the margin, in form and dimensions as described above; asci and ascospores as on malt agar. Initials of perithecia (fig. 144C) readily observed on cornmeal agar in the margins of developing colonies, consisting of thick, irregularly septate, and sometimes branched hyphae (as reported by Emmons, 1935).

Species description based upon many cultures showing the above cultural and morphological characteristics. Included in this number may be listed the following: NRRL 1017, from the Thom Collection as No. 4733.126.1, received from Biourge in 1924 as his No. 401 originally from Klöcker and presumably type; NRRL 1016 received in 1920 from L. H.

Bailey as an isolate from bread from Bangkok, Siam; NRRL 1018 received in 1930 from B. O. Dodge, New York Botanical Garden, as an isolate from Cuba; NRRL 1013, isolated from gingerale in Washington, D. C. in

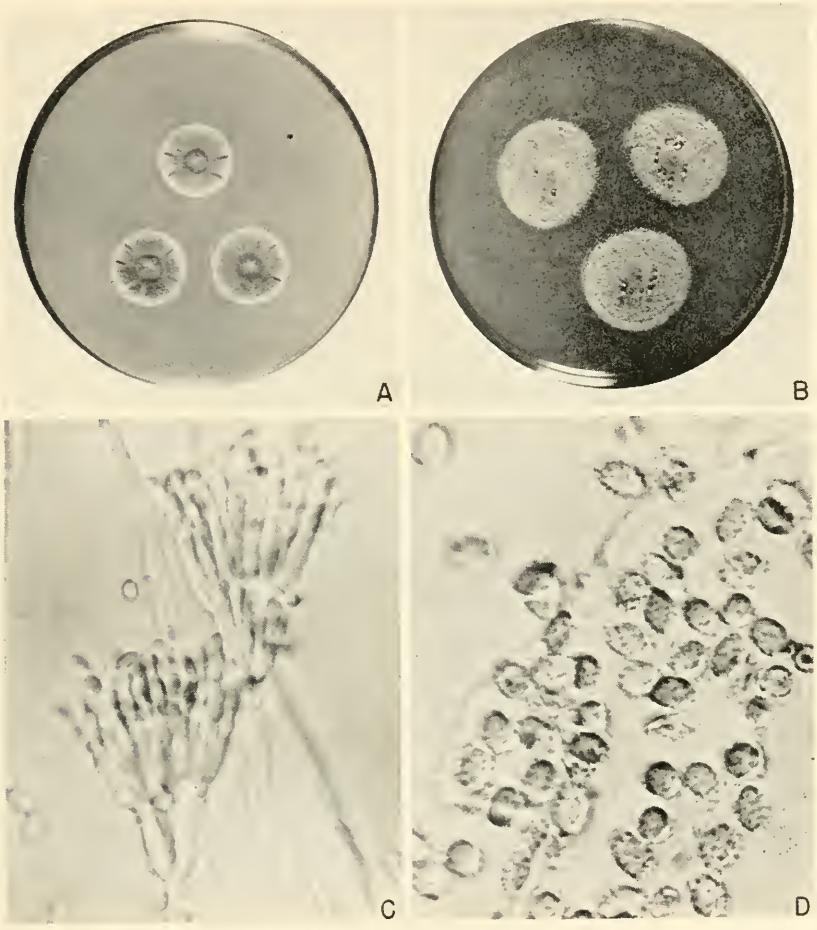


FIG. 149. *Penicillium wortmanni* Klöcker. *A* and *B*, Ten-day-old colonies of NRRL 1013 on Czapek and malt agars. *C*, Detail of two typical penicilli, × 1000; observe lanceolate pattern of sterigmata that is characteristic of the Biverticillata-Symmetrica section. *D*, Mature ascospores of NRRL 1017 showing elliptical form and rough spore walls that are characteristic of species, × 1500.

1940; NRRL 1614 from Harvard University as *Penicillium sulfureum* Sopp, contributed by F. A. Wolf, Duke University; and two strains received from the Centraalbureau as *Penicillium wortmanni* in June 1946. The species has been represented in the present study by 13 additional strains

recently isolated or received from such scattered original sources as Sweden, Brazil, South Africa, Panama Canal Zone, and England.

This species is one of, if not in fact, the most abundant of all the ascosporic Penicillia in nature. Representative strains have been regularly encountered in this Laboratory in soil population studies and have been received from many investigators abroad. It is apparently world-wide in distribution.

Penicillium wortmanni Klöcker is commonly confused with *P. vermiculatum* Dangeard. Thom (1930) regarded the two species as synonymous. He further concluded that his culture No. 11, which had been designated *P. luteum* Zukal originally (1910) upon the advice of Wehmer, represented *P. wortmanni* Klöcker. This opinion was shared by Biourge (1923). Derx (1926), studying the same culture, had observed the characteristic clavate ascogones and correctly identified it with Dangeard's *P. vermiculatum* (1910).

In his comparative study of ascocarp formation in the Penicillia, Emmons (1935) reported and figured significant differences in the perithecial initials of *Penicillium wortmanni* and *P. vermiculatum*, and his observations have been confirmed in our present study. In addition, we have found that cultures of *P. wortmanni* consistently produce more restricted and slower-growing colonies. Penicilli in the latter species are more regularly biverticillate and symmetrical, although in their most typical aspect they are strikingly similar in the two species. The conidia of *P. wortmanni* are usually slightly larger and more definitely pointed. In neither species can perithecia be said to develop a true wall, but strains of *P. vermiculatum* generally show a more definite bounding hyphal network than strains of *P. wortmanni*. Ascospores in the two species are strikingly similar but tend to be smaller and less conspicuously spinulose in *P. wortmanni*.

Unlike *Penicillium vermiculatum* Dangeard, *P. avellaneum* Thom and Turesson, and *P. stipitatum* Thom, which often lose the capacity to produce perithecia upon continued laboratory cultivation, all of the strains of *P. wortmanni* in our possession continue to produce some ascosporic structures. This capacity is substantially reduced in some of our strains that have been in the Collection for ten years or more, but in no case has it disappeared completely. Recent isolates usually develop both abundant perithecia and conidial structures.

Penicillium helicum Raper and Fennell, in Mycologia **40**: 515–518, fig. 3. 1948.

Colonies on Czapek's solution agar growing restrictedly, commonly not exceeding 1.5 to 2.0 cm. in 2 to 3 weeks at room temperature, comparatively thin (fig. 150A), with vegetative mycelium largely submerged and with sur-

face growth comparatively loose, almost floccose, in flesh to orange-pink shades, tardily developing conidial structures in limited numbers; rarely producing perithecia (see malt agar); odor not pronounced; exudate limited or lacking; reverse at first colorless, developing red shades in age; penicilli variable in pattern, mostly fractional, commonly monoverticillate, some-

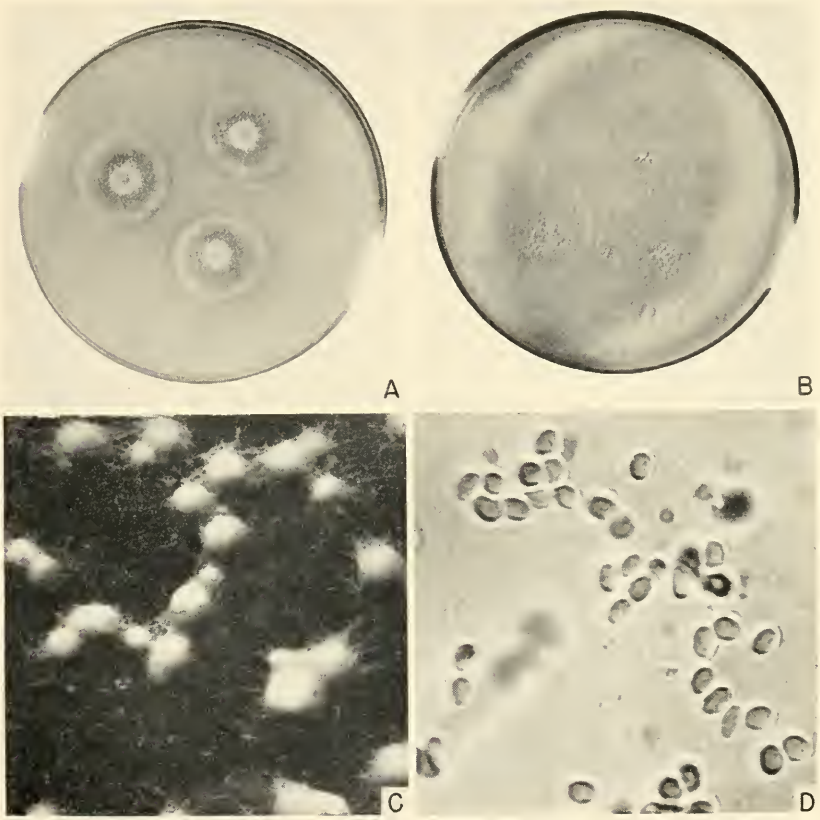


FIG. 150. *Penicillium helicum* Raper and Fennell, NRRL 2106. *A* and *B*, Ten-day-old colonies on Czapek and malt agars. *C*, Mature perithecia as seen on corn meal agar, × 30. *D*, Mature ascospores showing characteristic elliptical form, but failing to show delicate-echinulation, × 1500.

times branched and usually asymmetric, sometimes biverticillately-symmetrical in the manner characteristic of the series; conidiophores borne primarily as branches from aerial hyphae, commonly 100μ or less in length by 2.0 to 2.5μ, with walls smooth or irregularly roughened and colored in light yellow-green shades; metulae variable, when present commonly 10 to 15μ by about 2.0μ, rarely occurring in clusters of more than 3 or 4; sterig-

mata tapered in the manner characteristic of the group, produced in limited clusters up to 6 or 7, variable in dimensions, 8 to 12μ by 2.0 to 2.5μ, bearing conidia in short divergent chains; conidia elliptical, smooth, about 3.0 to 3.5μ by 2.5μ.

Colonies on malt extract agar spreading broadly, up to 6 to 7 cm. in 12 to 14 days, plane (fig. 150B), comparatively thin, consisting of a loose network of aerial mycelium in which soon develop abundant perithecia with accompanying encrusted and pigmented hyphae to give the colony a rich golden yellow color, in age near light cadmium to aniline yellow (Ridgway, Pl. IV); conidial structures lacking or limited in number, odor lacking; no exudate; reverse in brownish orange shades; perithecia generally spherical or nearly so (fig. 150C), ranging from 100 to 300μ in diameter, usually about 200 to 250μ, soft, sometimes confluent, without specialized cellular walls but bounded by thin interwoven hyphal networks, and surrounded by loose coverings of twisted or spiral, encrusted, and pigmented hyphae up to 150 to 200μ or more in length; asci produced abundantly throughout, borne in short chains, at maturity spherical to ovate, 5.5 to 7.0μ in diameter, 8-spored, ascus walls breaking down quickly to leave the perithecial cavity filled with free ascospores; ascospores small, elliptical, delicately spinulose over the entire surface (fig. 150D), about 2.5 to 3.0μ by 1.4 to 1.8μ.

Colonies on cornmeal agar spreading fairly broadly, 5 to 6 cm. in 2 weeks, vegetative mycelium largely submerged and producing scattered perithecia and limited conidial structures, mostly fractional.

Perithecial initials (fig. 144D) are readily observed upon most substrata, particularly upon cornmeal agar. They first appear as thickened, club-shaped hyphae (ascogonia?) around the bases of which coil much thinner hyphae (antheridia?). These latter hyphae confine themselves to the basal areas of the club-shaped structures and usually terminate as slight enlargements closely appressed against the walls of the larger hyphae. The club-shaped hyphae apparently elongate and soon begin to coil terminally, at first in loose helix-like patterns and subsequently as rather tight spirals. As the spirals continue to develop, their identities are soon lost in developing knots of interwoven tissue. We have not succeeded in establishing whether these knots develop primarily by the septation and repeated branching of the coiled structures or by the proliferation of adjacent hyphae. The developmental history of the perithecium has not been elucidated, but the origin and pattern of ascus formation can be fairly well worked out in the ripening perithecium.

Species description based upon NRRL 2106 as type; isolated originally from soil from Sweden sent to us by Professor Edy Velander.

Penicillium helicum is distinguished from other members of the *P. luteum*

series by the coiled helix-like pattern of its perithecial initials and the small dimensions of its ascospores. When young the perithecial initials are strongly suggestive of *P. vermiculatum*, but as these develop they assume a markedly different and specific pattern.

The name, *Penicillium helicum*, is based upon the characteristically coiled structures that distinguish the species, and is taken from the Latin *helica*, meaning winding.

Penicillium sacchari Ray (Rev. Gen. Bot. **9:** 294–300; Pl. 16, figs. 23–27. 1897) may have represented some form approximating the above species. Perithecia were reported as fairly abundant, with mycelial masses yellow to orange. Penicilli were biverticillately symmetrical, and conidia quite small, 2.0 by 1.0μ. Asci were said to be 6-spored, with spores heavy-walled and measuring 3.0 by 2.5μ. The species has not been reported since it was described.

Penicillium spiculisporum Lehman, in Mycologia **12:** 268–274, Pl. 19, figs 1–37. 1920. See also Thom, The Penicillia, pp. 452–454. 1930; Emmons, Mycologia **27:** 135–136, figs. 3 and 16. 1935.

Colonies on Czapek's solution agar growing restrictedly (fig. 151A), about 1.5 to 2.0 cm. in two weeks at room temperature, consisting of a tough mycelial felt about 0.5 mm. deep, with surface appearing lightly floccose, in white to light cream shades, azonate, conidial structures usually not produced, if present few in number and not affecting the colony appearance; perithecia often not produced or, if produced, late in appearing; exudate generally lacking; odor pronounced, fragrant; reverse at first colorless, gradually assuming flesh to yellowish shades.

Colonies on steep agar growing more rapidly, about 4.5 to 5.0 cm. in two weeks, comparatively thin, loose-textured with surface appearing floccose to almost funiculose when examined under low magnifications, showing a tendency to develop radial sectors, light to medium sporing throughout, producing a light grayish green coloration except in the growing colony margin; perithecia produced in limited numbers adjacent to the substratum, partially obscured by the overlying vegetative mycelium and conidial heads; odor pronounced, suggesting mushrooms; reverse in yellowish pink shades; penicilli variable, from monoverticillate through irregular patterns to typically biverticillate-symmetrical, usually borne on short conidiophores arising as branches from aerial hyphae; conidiophores commonly less than 50μ in length by 1.8 to 2.2μ in diameter, smooth-walled; metulae lacking or few in the verticil, rarely 4 or more, commonly irregularly arranged, 10 to 15μ by 1.8 to 2.2μ; sterigmata closely parallel, mostly 5 to 8 in the verticil, 10 to 12μ by 1.5 to 2.0μ, characteristically tapered; conidia strongly elliptical, 2.5 to 3.0μ by 1.5 to 2.0μ, thin-walled, smooth.

Colonies on malt extract agar growing fairly rapidly (fig. 151B), about

4.5 to 5.0 cm. in two weeks, thin, white, with vegetative mycelium largely submerged but evident as a loose aerial network ranging from cream to golden yellow in color; producing abundant perithecia mostly adjacent to the agar surface and usually forming a continuous layer, but sometimes less abundant or lacking in limited sectors; perithecia spherical to oblong (fig.

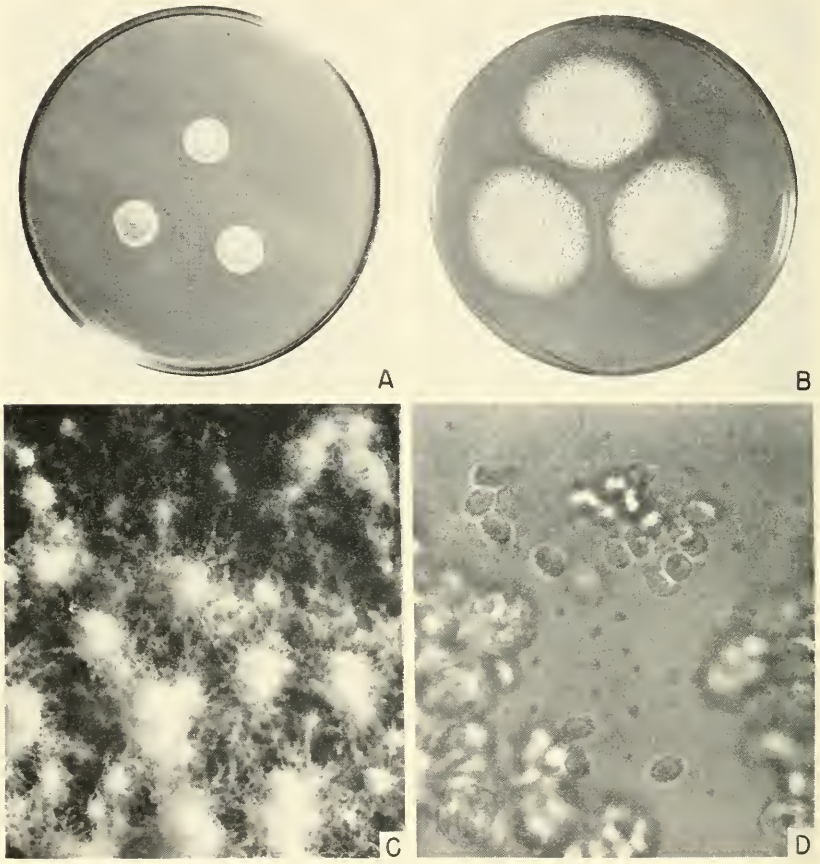


FIG. 151. *Penicillium spiculisporum* Lehman. *A* and *B*, Ten-day-old colonies of NRRL 1028 on Czapek and malt agars. *C*, Perithecia as seen on steep agar, × 30. *D*, Mature ascospores and asci, × 1500.

151C), variable in size up to 350 to 400μ in diameter, white to dull cream in color often becoming yellow in age, characterized by a fairly definite wall of closely interwoven hyphae, surrounded by a loose mantle of heavy, encrusted radiating hyphae to produce a bristly appearance under low magnifications; perithecium containing a hyphal network bearing abundant asci in short chains; asci oval to sub-spherical when mature, about 6.0 to

7.0μ in diameter, 8-spored; ascospores elliptical, spinulose over the entire surface (fig. 151D), 3.0 to 3.5μ by 2.2 to 2.8μ, colorless. Conidial structures limited in number, as described above.

Colonies on cornmeal agar up to 4.0 to 4.5 cm. in two weeks, very thin, vegetative mycelium submerged, perithecia fairly abundant in central colony areas, thinning toward the margin, in form and texture as described on malt agar, penicilli few in number, not affecting the colony appearance.

Perithecial initials (fig. 144E) are easily recognized on cornmeal agar, and, as described by Emmons (1935), usually appear as conspicuously swollen and irregularly branching sections of aerial hyphae.

Species description centered upon numerous strains regarded as typical of the species. Included among these are NRRL 1028, received in 1937 from C. W. Emmons; NRRL 1026 maintained in the Thom Collection without change since 1919; NRRL 1029 received in 1939 from Professor Leva B. Walker, University of Nebraska; and two cultures received from the Centraalbureau under this name in the spring of 1946. In addition to the above, six other strains recently isolated or received for identification duplicate them in all essential characters. Strains examined have included isolates from various stations in the United States and abroad. The species is typically a soil form and appears to be widely distributed.

In marked contrast to NRRL 1026, which has been maintained in culture for 28 years without losing its capacity to produce an ascosporic stage, other strains have lost their capacity to produce perithecia in relatively short periods of laboratory cultivation.

If examined superficially, this species might easily be mistaken for a member of the Monoverticillata. Sterigmata commonly occur in simple unbranched verticils and are often borne on relatively short conidiophores that arise from trailing aerial hyphae. However, upon careful examination, the sterigmata are seen to be tapered in the manner typical of the Biverticillata-Symmetrica, and the penicilli to range from simple monoverticillate, through irregularly asymmetrical to typical biverticillate and symmetrical structures. Assignment in its present position is based upon the character of its sterigmata and upon the maximal pattern of development shown by its penicilli. The correctness of this placement is substantiated by the form, development, and character of its perithecium, which lacks a definite specialized cellular wall, and by the pattern of the ascospores produced.

Penicillium rotundum Raper and Fennell, in Mycologia, **40**: 518–521, fig. 4. 1948.

Colonies on Czapek's solution agar growing very restrictedly (fig. 152A), about 1.0 cm. in 2 weeks at room temperature, consisting of a compact, fairly tough felt up to 500μ or more deep, at first appearing largely mycelial

but developing abundant inconspicuous perithecia (see malt agar) after one week to 10 days and showing bright golden-yellow shades from pigmentation of the perithecia and the encrusted hyphae surrounding them; penicilli generally lacking or, if present, limited in number and usually fragmentary (see 20 per cent sucrose-Czapek), not affecting the colony appear-

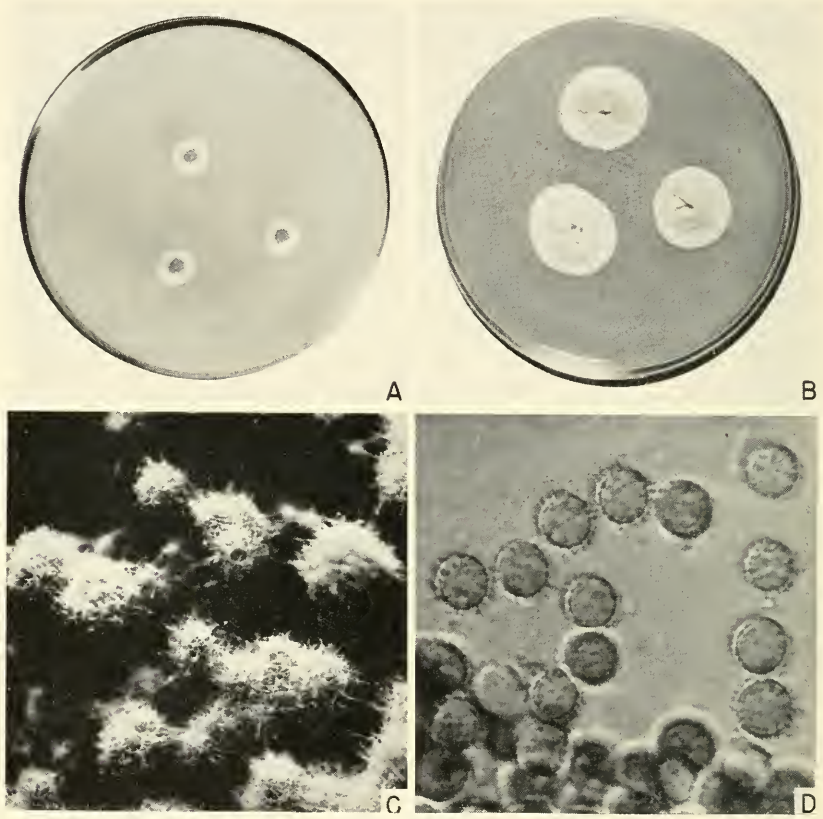


FIG. 152. *Penicillium rotundum* Raper and Fennell, NRRL 2107. *A* and *B*, Ten-day-old colonies on Czapek and malt agars. *C*, Mature perithecia on malt agar, × 30. *D*, Ripe ascospores showing characteristic globose form and conspicuously roughened walls, × 1500.

ance; exudate limited, light amber in color; odor slight or lacking; reverse in yellow to orange-red shades with surrounding agar lightly colored.

Colonies on Czapek's solution agar with 20 per cent sucrose growing restrictedly as above, plane, producing abundant conidial structures in a dense stand, velvety or nearly so, in pale gray-green shades near olive-gray (Ridgway, Pl. LI) to storm gray (R., Pl. LII), conidiophores arising pri-

marily from the substratum, comparatively short, seldom exceeding 200μ in length by 3.0μ in diameter; penicilli variable, ranging from fractional or monoverticillate to typical biverticillate-symmetrical; metulae in limited verticils, rarely exceeding 4 in number, 10 to 13μ by 2.0 to 2.5μ; sterigmata closely parallel, in clusters of 4 to 6 or 7, about 10 to 12μ by 1.5 to 2.0μ, with conidium-bearing tips definitely tapered in the manner characteristic of the group; conidia elliptical, with ends more or less pointed, mostly 2.5 to 3.0μ by 2.0 to 2.5μ, smooth-walled.

Colonies on malt extract agar growing slowly (fig. 152B), 1.5 to 2.0 cm. in 2 weeks, in bright golden yellow shades near lemon-chrome to light cadmium (R., Pl. IV), with growing margin 1 to 2 mm. wide, thin, often largely submerged, quickly developing abundant perithecia to form a continuous layer which in the main constitutes the colony; perithecia usually globose or nearly so (fig. 152C), but varying greatly in size from 150 to 300 or 350μ in diameter, sometimes confluent, without definite cellular walls, bounded by a thin network of interwoven hyphae and surrounded by a loose covering of predominantly radiate, heavily encrusted, and strongly pigmented hyphae, 100μ or more in length; perithecia ripening within 7 to 10 days, producing abundant asci throughout; asci borne in short chains, ovate to globose when mature, 12.5 to 15.0μ in diameter, 8-spored; ascospores globose (fig. 152D), definitely echinulate over the entire surface, mostly 4.5 to 5.0μ in diameter, with walls heavy, 1.0μ or more thick.

Colonies on cornmeal agar slow-growing, about 2 cm. in 2 weeks, thin with mycelium largely submerged, producing perithecia abundantly at colony center and scattered throughout the entire colony area, in form and development as on malt; penicilli very limited in number.

Perithecial initials (fig. 144F) readily observed at the margin of growing colonies upon most substrata, particularly cornmeal and malt extract agars, irregular in origin and pattern (not consistent as in *Penicillium vermiculatum*, *P. helicum*, and *P. stipitatum*), first evident as swollen and irregularly septate hyphal elements which may be more or less twisted or coiled and which may arise either directly from vegetative hyphae or from structures at first appearing penicillate, quickly developing into a knot of twisted and interwoven hyphal elements. Definite ascogones are usually not identifiable.

Species description based upon NRRL 2107 as type received in March 1946 from Professor G. W. Martin, University of Iowa, as an isolate from wood collected in the mountains of Chiriqui Province, Panama. The species is distinguished by its restricted growth upon all substrata, the rich golden yellow color of its massed perithecia, the variability of its perithecial initials, and particularly by its large globose ascospores. The specific name was based upon the shape of the ascospores.

The species is believed to be more closely related to *Penicillium wortmanni* than to other members of the *P. luteum* series. It differs from *P. wortmanni* principally in the character of its perithecial initials and its globose ascospores. In form, the latter are similar to the spores of *P. bacillosporum* Swift but are consistently larger. It is readily distinguished from the latter species by differences in habits of growth, coloration, and particularly conidial patterns.

Penicillium bacillosporum Swift, in Bul. Torrey Botanical Club **59:** 221–227, fig. 1, a to g. 1932. Emmons, Mycologia **27:** 136, figs. 2 and 16. 1935.

Swift's diagnosis as follows:

"Mycelium funiculose showing marked color differences on different nutrients, from pale yellow on cornmeal to salmon on dextrose agar. Chromogenic effects in the medium itself also varied from bright green in cornmeal agar to red in dextrose agar.

"Conidia 3–6 x 1.5μ, bacillar, not numerous, in long diverging thread-like chains, persistent at first, fragmenting in age. Penicillus predominantly monoverticillate, but occasionally biverticillate. Sterigmata 10–15 x 2.5–3.5μ, five or six in a whorl. Conidiophores short, 25–50 x 3–5μ, branched, formed mostly at right angles to the trailing, sometimes funiculose, hyphae.

"Perithecia averaging 137–150μ in diameter, usually whitish to pale yellow, with thin but definite walls of interlacing hyphae. Asci 10–12.5 x 7.5–10μ, globose, oval or pear-shaped, 8-spored. Ascospores 3.5–4μ, globose, finely verrucose, hyaline to yellowish in age.

"On Begonia leaf, probably saprophytic.

"Type locality, New York City."

Additional notes based upon Swift's original species description and upon our observations of the type culture:

Colonies on Czapek's solution agar growing somewhat restrictedly, consisting of a velvety aerial felt more or less buckled, pale yellow throughout, often developing a slight green tinge at extreme center, later becoming sulphur yellow in the center with pale yellow to orange droplets; reverse at first dark and indefinite, later becoming green at colony edge. Both perithecia and conidial structures produced but often in limited numbers.

Colonies on malt extract agar spreading, about 5 cm. in diameter in 2 weeks at room temperature, plane, fairly thin, consisting of a fairly loose aerial felt of somewhat funiculose hyphae in which are embedded abundant perithecia near the agar surface and upon which are borne scattered to fairly numerous conidial structures, mostly monoverticillate, occasionally biverticillate and symmetrical.

Colonies on cornmeal agar spreading, showing little aerial growth except around the very pale yellowish perithecia which dot the surface of the colony after a few days; mycelium almost entirely submerged and hyaline; reverse

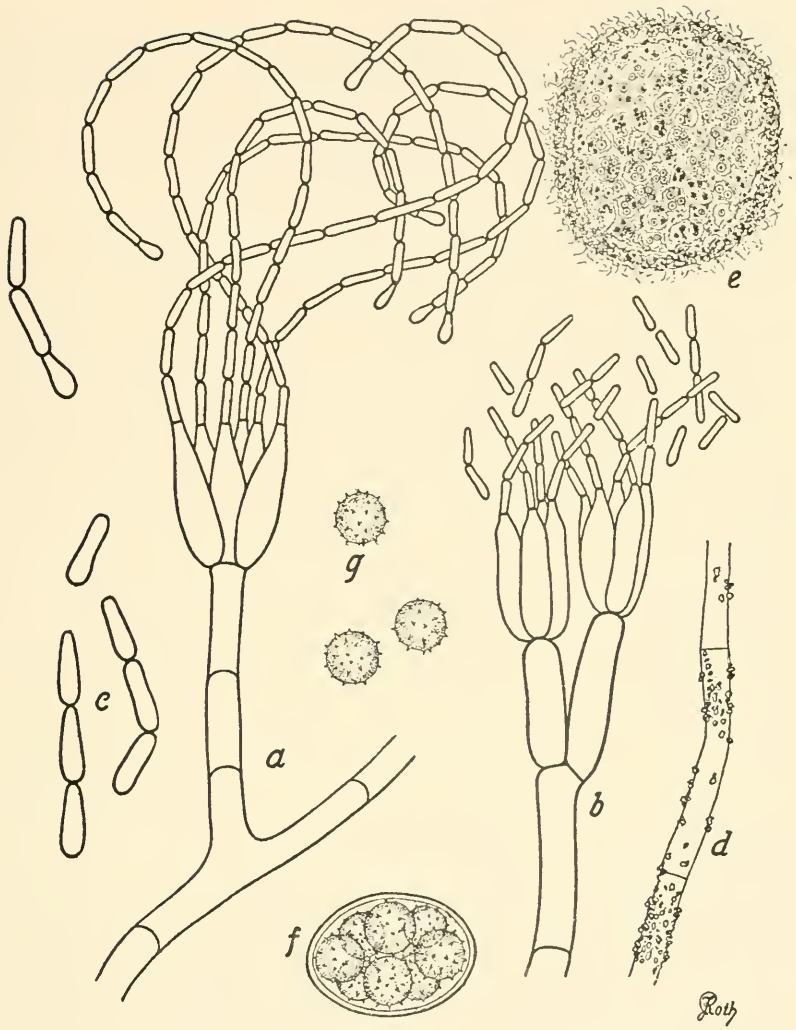


FIG. 153. *Penicillium bacillosporum* Swift. *a*, Typical conidiophore with spore chains. *b*, Branched conidiophore. *c*, Individual conidia. *d*, Hypha with yellow granules. *e*, Section of ascocarp showing asci and two-layer wall. *f*, Ascus with ascospores. *g*, Individual ascospores. (After Swift, Torrey Bot. Club Bull., *59*, 1932.)

and substrate in certain areas become bright to deep green; conidial structures fairly abundant, produced on trailing hyphae or ropes of hyphae chiefly near the perithecia.

As reported and illustrated by Swift (fig. 153), conidiophores are short, and are usually borne at right angles to the main hyphae; conidiophore walls sometimes show a slight roughening. Penicilli are variable. Sterigmata

occur usually in simple verticils of five or six. They are typically acuminate to lanceolate, hence characteristic of the Biverticillata-Symmetrica section of the genus. A single side branch frequently occurs, suggesting a biverticillate condition, or two, three, or rarely more shorter branches may form a true verticil of metulae and constitute a definitely biverticillate penicillus. The conidia are unique among the Penicillia. They are rod-like in form, 3 to 6μ by 1.0 to 1.5μ, becoming slightly larger at one end with maturity, and in very old cultures approaching an oval contour. The terminal spore of each chain is consistently shorter than the others and nearly oval. They develop in long divergent and tangled thread-like chains which break up readily in old cultures but are quite persistent when young, at which time the individual spore limits are often barely discernible. Perithecia are approximately globose, non-ostiolate, average about 137 to 150μ in diameter, and are surrounded by a loose net of branching roughened hyphae usually pale yellowish in color. Asci begin to show mature ascospores within twelve to fifteen days on cornmeal agar at room temperature. Ascospores are spherical, 3.5 to 4.0μ in diameter, very finely verrucose, at first hyaline, but in age may show an orange-yellow tint. Upon germination they swell to about twice their normal size and send out one or two germ tubes (*fide* Swift). The mycelium is hyaline, branching, septate, 2.5 to 4.0μ, and often roughened with yellowish deposits particularly about the perithecia.

Emmons (1935) reported and figured the perithecial initials of this species as a pair of short coiled hyphae. In our examination of the type, we have observed structures which seem to fit this interpretation. We have not, however, succeeded in establishing, with certainty, that perithecia develop from the coiled structures observed in our cultures.

The species is represented only by the type strain. It was received from Swift prior to the publication of her species, and has been continued in laboratory culture since that time. It is now maintained in our Collection as NRRL 1025. The culture, as examined during the current study, differs from its original aspect only in producing relatively fewer perithecia on Czapek agar and apparently ripening ascospores somewhat more tardily.

The species is distinguished by the bacillary form of its conidia, from which it takes its name. It is also characterized by the production of globose, echinulate ascospores, a pattern unique to this species and *Penicillium rotundum*, recently described by Raper and Fennell (1948). The production of penicilli that are usually monoverticillate suggests relationship to the ascosporic series of the section Monoverticillata. Such a placement, however, is counter-indicated by the presence of lanceolate to acuminate sterigmata (characteristic of the Biverticillata-Symmetrica) and the formation of perithecia bounded by a network of interwoven hyphae rather

than a definitely specialized cellular wall. We believe the species should be retained in the Biverticillata-Symmetrica where Swift originally assigned it upon the advice of Thom.

Penicillium avellaneum Thom and Turesson, in Mycologia **7:** 284–287, figs. 1, 2. 1915. Thom, The Penicillia, pp. 446–447, fig. 70. 1930.

Colonies upon Czapek's solution agar spreading broadly (fig. 154A), up to 6.0 to 7.0 cm. in 12 to 14 days at room temperature, lanose to velvety, becoming somewhat floccose in central colony areas, up to 2 mm. or more deep, medium to light sporing throughout, heavier in marginal areas, with conidial areas becoming persistently avellaneous (Ridgway, Pl. XL), in new isolates characteristically producing perithecia slowly during a period of several weeks accompanied by the gradual development of limited aerial hyphae colored Indian red (R., Pl. XXVII), in older stock cultures commonly failing to develop either perithecia or red hyphae; exudate limited, in vinaceous shades; odor not pronounced; reverse in deep red shades near Indian red, with agar similarly colored in lighter shades; conidiophores arising primarily from the substratum up to 400μ long by 3 to 5μ in diameter, smooth-walled, terminated by conidial structures bearing tangled chains of conidia up to 200μ long; penicilli variable, typically compact, consisting of a crowded terminal verticil of numerous metulae 8 to 10μ by 3 to 4μ or more (fig. 143C), bearing verticils of 5 or more sterigmata 7.5 to 9.0μ by about 2.0μ, or with branches (metulae) more or less irregularly disposed over the terminal 10 to 20μ of the conidiophore; conidia ellipsoid to almost globose, 3.0 to 4.0μ or even 5.0μ by 2.0 to 3.0μ, smooth, often appearing heavy-walled; perithecia usually scantily produced, globose or nearly so (fig. 154C), up to 400 or 500μ in diameter, commonly smaller, without a specialized cellular wall but bounded by an interwoven network of mycelial elements, one or more cells thick, characteristically developing asci throughout the central network of fertile hyphae, more or less brittle in age; asci borne singly on short branches, ovate, about 12 to 15μ by 9 to 10μ, 8-spored; ascospores ellipsoid, 6.0 to 7.5μ by 4.0 to 5.0μ, with walls thick, appearing double, pitted or with the appearance of round, transparent spots (fig. 154D).

Colonies on malt extract agar (Col. Pl. IX) spreading broadly, 6 to 7 cm. (fig. 154B) in most strains in 10 to 12 days; new isolates typically produce abundant perithecia in bright yellow shades against a background of deep reddish or reddish purple mycelium intermixed with light brown (avellaneous) conidial structures to produce a characteristic appearance; old and usually non-ascosporic stocks are uniformly avellaneous throughout from abundant conidial development; perithecia and conidial structures as described above.

Colonies on corn meal agar spreading broadly, thin, with mycelium largely submerged, producing scattered conidial structures and typical perithecia throughout the entire colony but more abundantly in colony margins, little pigment produced.

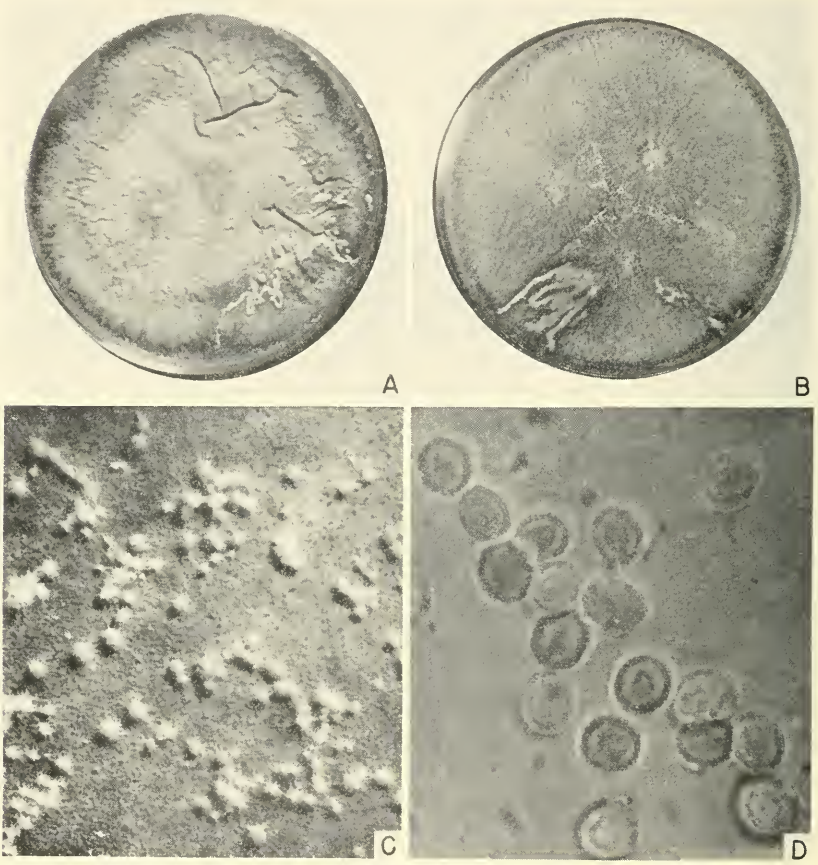


FIG. 154. *Penicillium avellaneum* Thom and Turesson. *A* and *B*, Two-week-old colonies of NRRL 2108 on Czapek and malt agars; perithecia are rather sparsely produced and are usually most evident along intersecting colony margins. *C*, Perithecia as seen with low magnification, × 5. *D*, Ripe ascospores showing typical elliptical form and thick, pitted walls, × 1500.

The pattern of the perithecial initials has not been established definitely, since ascosporic structures usually develop well within the margins of established colonies.

Species description centered upon NRRL 1938 isolated in September 1943 from soil from San Antonio, Texas; and NRRL 2108, received in

August 1945, from Dr. Ralph Emerson as an isolate from retting guayule shrub, Salinas, California. Both of these cultures produce abundant perithecia upon most substrata and are regarded as wholly typical of the species. The species is also represented by NRRL 1005 (Thom, No. 4401) received in 1930 as an isolate from cereal products, Guatemala City, Guatemala. When first isolated this culture produced abundant perithecia and ascospores and was cited by Thom in his Monograph (1930, p. 447), but the ascosporic phase has been lost during the ensuing years. The strain was sent to the Centraalbureau by Thom in 1930 and was returned to us for the present study in February 1946. Their substrain is now predominantly conidial but when cultivated upon corn meal agar still produces occasional small perithecia which develop limited numbers of typical asci and ascospores. It is included in our Collection as NRRL 2109. Other strains have been examined from Puerto Rico, China, Panama, and various stations in the United States. The species is not abundant but appears to be widely distributed. Members of this species, even more than most other members of the *Penicillium luteum* series, tend to lose their capacity to produce perithecia when long maintained in artificial culture.

In their original description, Thom and Turesson described and figured the perithecium as bounded by a definite and continuous cellular wall or peridium, one cell in thickness. The ascosporic strains examined in the present study fail to develop this specialized structure and show instead a closely interwoven mycelial covering not markedly different from that seen in *Penicillium vermiculatum* Dangeard, *P. stipitatum* Thom, *P. striatum* Raper and Fennell, and others. *Penicillium avellaneum* is believed to be properly assigned in the *P. luteum* series upon the basis of its perithecial structures. It differs from other members of the series by producing (1) coarse hyphae in greater or less abundance which develop reddish purple colors near Indian red, (2) ascospores with heavy, pitted walls, and (3) conidial structures which, although often biverticillately-symmetrical in pattern, differ substantially from the typical penicilli of this group. Metulae are often produced in considerable numbers, up to 8 or 10 or more, and sterigmata fail to show the lanceolate pattern characteristic of this section of the genus. Upon the basis of the conidial structures alone, one might be tempted to assign this species to the Brevi-Compacta series (see p. 404).

Penicillium ingelheimense van Beyma, in Antonie van Leeuwenhoek J. Microbiol. Serol. **8**: 109. 1942. This species, as it is represented in our cultures upon different substrata, appears to be an unusually coarse strain of *P. avellaneum* T. and T. Conidiophores are commonly 500μ or more in length and in terminal areas may reach a diameter of 7 to 8μ. In liquid mounts walls appear smooth but when examined dry show some evidence of roughening (adherent material?). The penicilli are unusually large and the number of metulae present in some structures is estimated to range up

to 12 to 15. As in typical strains of *P. avellaneum*, metulae commonly arise not as a true verticil at the tip of the conidiophore but over a considerable portion of the terminal area; measurements of metulae, sterigmata, and conidia duplicate those of *P. avellaneum*. Colonies spread broadly upon all media tested, sporulate abundantly, and produce conidial areas in true avellaneous shades. We have observed no evidence of an ascosporic phase. The type strain is maintained in our Collection as NRRL 2110.

Penicillium luteum Zukal, in Sitz.-Ber. Akad. Wein. **98:** 561. 1889; Thom, U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, pp. 39–42, fig. 8. 1910; Thom, The Penicillia, pp. 448–449. 1930; Emmons, Mycologia **27:** 141–143, figs. 10 and 16. 1935.

Colonies on Czapek's solution agar growing rather restrictedly, attaining a diameter of 2.5 to 3.5 cm. in 2 weeks, consisting of a comparatively thin, tough mycelial felt with surface appearing slightly fibrous, azonate or slightly zonate, strongly wrinkled and buckled (fig. 155A), sometimes splitting, at first colorless to yellowish but soon developing orange-red shades and often showing superficial tufts of bright yellow hyphae, often developing few perithecia or conidial structures (see malt agar); exudate lacking or very limited; odor evident, sweetish; reverse in bright orange-red shades.

Colonies on steep agar growing somewhat more rapidly than on Czapek, more highly colored, and commonly developing bright yellow-green shades from pigmentation of superficial hyphae, often not associated with conidial structures; small, fractional penicilli sometimes produced in limited numbers; perithecia lacking.

Colonies on malt extract agar very restricted (fig. 155B), about 1.5 to 2.0 cm. in 2 weeks, raised, 1 mm. deep, comparatively tough, commonly consisting of an interwoven mycelial felt bearing a continuous surface layer of massed perithecia and enveloping sterile hyphae, bright yellow in color, near lemon yellow to lemon chrome (Ridgway, Pl. IV); conidial structures often lacking or few in number, sometimes abundantly produced throughout the entire growth or in localized areas and sectors, sometimes dominating the colony appearance, in yellow-green, near pea green shades (R., Pl. XLVII); penicilli extremely variable, ranging from irregular aggregates of few sterigmatic cells to biverticillate structures that are often irregularly branched, occasionally almost symmetrical; metulae often lacking or difficultly identified; sterigmata variable in origin and dimensions, ranging from 8 to 12μ or even 15μ in length by 2.5 to 3.0μ but consistently tapered in the manner characteristic of the group; conidia elliptical to ovate, mostly 2.5 to 3.0μ by 1.5 to 2.0μ; odor as on Czapek; reverse in dull brown shades; perithecia variable in form and dimensions, often confluent, when borne separately appearing rounded, oblong, or elongate, mostly 200 to 350μ in diameter, bounded by loose mycelial networks but without definite walls,

surrounded by limited to fairly extensive envelopes of irregularly twisted or coiled, bright yellow, encrusted mycelium (fig. 155C); asci abundantly produced throughout the body of the perithecium, apparently borne in clusters as buds from fertile hyphae (*fide* Emmons), sub-spherical to elongate when mature, 10 to 12μ in long axis, 8-spored; ascospores elliptical,

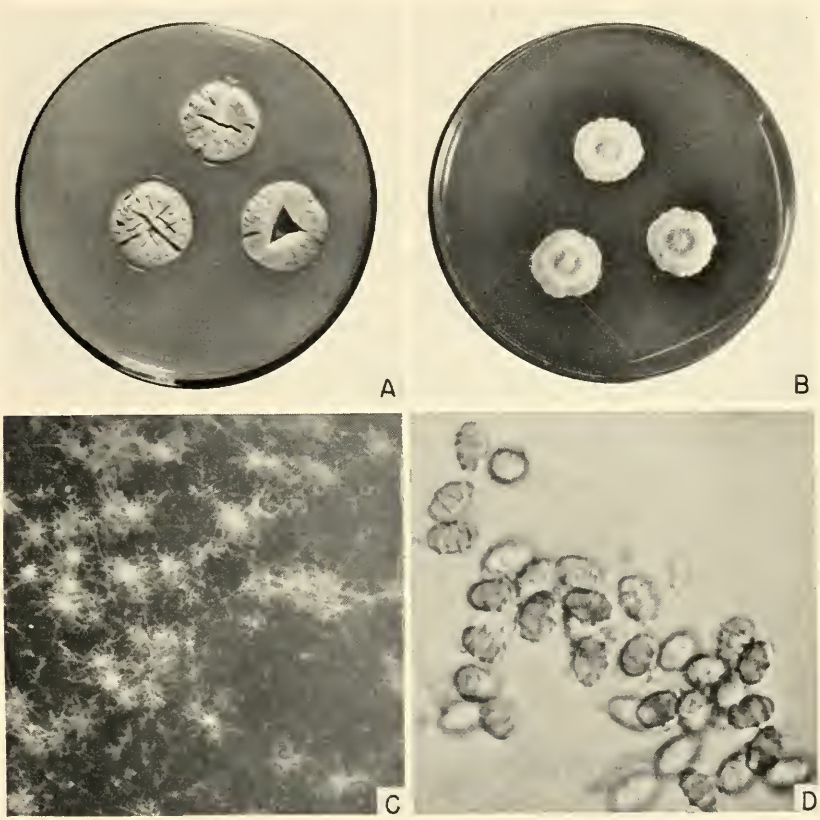


FIG. 155. *Penicillium luteum* Zukal. *A* and *B*, Two-week-old colonies of NRRL 1010 on Czapek and malt agars. *C*, Scattered, small perithecia of NRRL 2102 on corn meal agar, × 25. *D*, Ripe ascospores showing the characteristic banding described by Zukal, × 1500.

about 4.2 to 4.8μ by 2.2 to 2.8μ with conspicuous spiral bands that appear transverse as originally described by Zukal (fig. 155D), slightly yellow.

Colonies on corn meal agar up to 3.0 to 3.5 cm. in 2 weeks, growing sparsely with vegetative mycelium largely submerged, producing perithecia in limited numbers and only in central colony areas, in form, dimensions, and structures as described above; conidial structures lacking or limited in

number, fragmentary. Perithecial initials are composed of a pair of short coiled hyphae which complete one or two turns, and around which the ascocarp develops directly (*fide* Emmons).

Species description based upon NRRL 1010, from the Thom Collection as No. 5357.208, received in 1933 from Professor G. R. Bisby, University of Manitoba, Winnepeg, as an isolate from soil. This culture was included in Emmons' study (1935), and formed the basis for his observations and comments regarding *Penicillium luteum* Zukal. It was sent to the Centraalbureau by Thom in 1936 and was returned to us by them in June 1946. The two substrains remain essentially alike but the latter produces perithecia in somewhat greater abundance, hence, is maintained in our Collection as a separate accession, NRRL 2102. This culture is believed to closely approximate the form studied originally by Zukal. Insofar as we are aware, this culture represents the third or fourth strain of Zukal's species reported since *P. luteum* was described almost 60 years ago. Wehmer (1893) discussed a culture with transversely banded ascospores, although he subsequently identified Thom's No. 11 (with spinulose ascospores) as representing Zukal's species. Derx (1925, 1926) seems to have had a culture that conformed with Zukal's description, and it was in this culture that he reports having demonstrated heterothallism. Insofar as we know, Derx's observations have not been confirmed by other investigators, although his report seems entirely credible. Studying a different strain, than that upon which Derx's observations were based, Emmons failed to secure evidence of heterothallism and reported the production of abundant ascospores in cultures derived from single spores. Strain variation may possibly account for the contradictory reports. In any case, there is great need of additional study on this matter.

There has been much speculation as to the characteristics of Zukal's species, and various types of ascosporic Penicillia which produce yellow colonies have been assigned to it. The species was discussed by Wehmer in 1893 and again in 1897. We do not know the type of culture with which he worked, but we do know that in 1905 he identified Thom's strain No. 11 as *Penicillium luteum* Zukal, and it was so published by Thom (1910). Additional study and the examination of other cultures subsequently led Thom to regard it as *P. wortmanni* Klöcker (Thom, 1930, p. 448). It is now recognized as *P. vermiculatum* Dangeard (see p. 583). When it was still ascosporic, the culture in question produced elliptical, spinulose spores in contrast to the banded spores reported by Zukal. The rediscovery of cultures producing banded ascospores has reaffirmed the validity of Zukal's species as originally reported. The name is applied to the series of biverticillate-symmetrical Penicillia producing ascospores because it is at one

and the same time the oldest of the specific names and the most generally descriptive.

An additional culture, NRRL 2103, isolated from Swedish soil in January 1946, produces ascospores with transverse banding less marked but strongly suggestive of *Penicillium luteum* as described above. It differs from NRRL 1010, however, in producing more rapidly growing and less highly pigmented colonies. It also produces typical biverticillate-symmetrical penicilli in abundance upon most substrata. This culture is not regarded as representing the species *P. luteum* Zukal, and its proper assignment remains in doubt. We believe, however, that forms similar to this —should they be encountered by others—can be more easily located here than elsewhere. It is, therefore, tentatively considered adjacent to *P. luteum* upon the character of its ascospores. The isolation and examination of additional cultures may tend to lessen the significance of a spore character now regarded as unique and diagnostic. For the present, however, ascospores with transverse bands are reported only in the single species, *P. luteum*.

Penicillium striatum Raper and Fennell, in Mycologia, **40**: 521–524, fig. 5. 1948; also Williams, Cameron, and Williams in Food Research **6**: 69–73. 1941.

Colonies on Czapek's solution agar growing very restrictedly (fig. 157A), attaining a diameter of 1 to 1.5 cm. in 2 weeks at room temperature, with margin uneven from the irregular and localized growth of the vegetative mycelium, growing deeply in the agar with aerial hyphae and later perithecia developing above this deep mycelial growth, white to pale buff in color, with surface mealy or granular, conidial structures very limited in number and not affecting the colony appearance, vegetative mycelium comparatively coarse with hyphal tips at colony margin often showing inflated cells, perithecia abundantly produced, developing throughout the entire colony area, loose-textured, cottony, without definite cellular walls, ranging up to 100 to 150μ in diameter (figs. 156E and 157C); exudate not produced; odor lacking or indefinite; reverse at first colorless becoming dull brown in age; penicilli very sparsely produced (see colony description on 20 per cent sucrose Czapek). Perithecia ripening rather quickly with asci containing immature spores within 7 to 8 days and with ripe ascospores present in 12 to 14 days; asci apparently arising as branches from fertile hyphae, not in chains (figs. 156D and 157E), oblong to spherical, about 15μ in diameter, 8-spored; ascospores comparatively large, elliptical, with over-all dimensions ranging from 7.0 to 8.5 by 5.0 to 6.0μ, with walls bearing a series of wavy, longitudinal flanges or frills (fig. 157F), about 1.0μ in width, usually

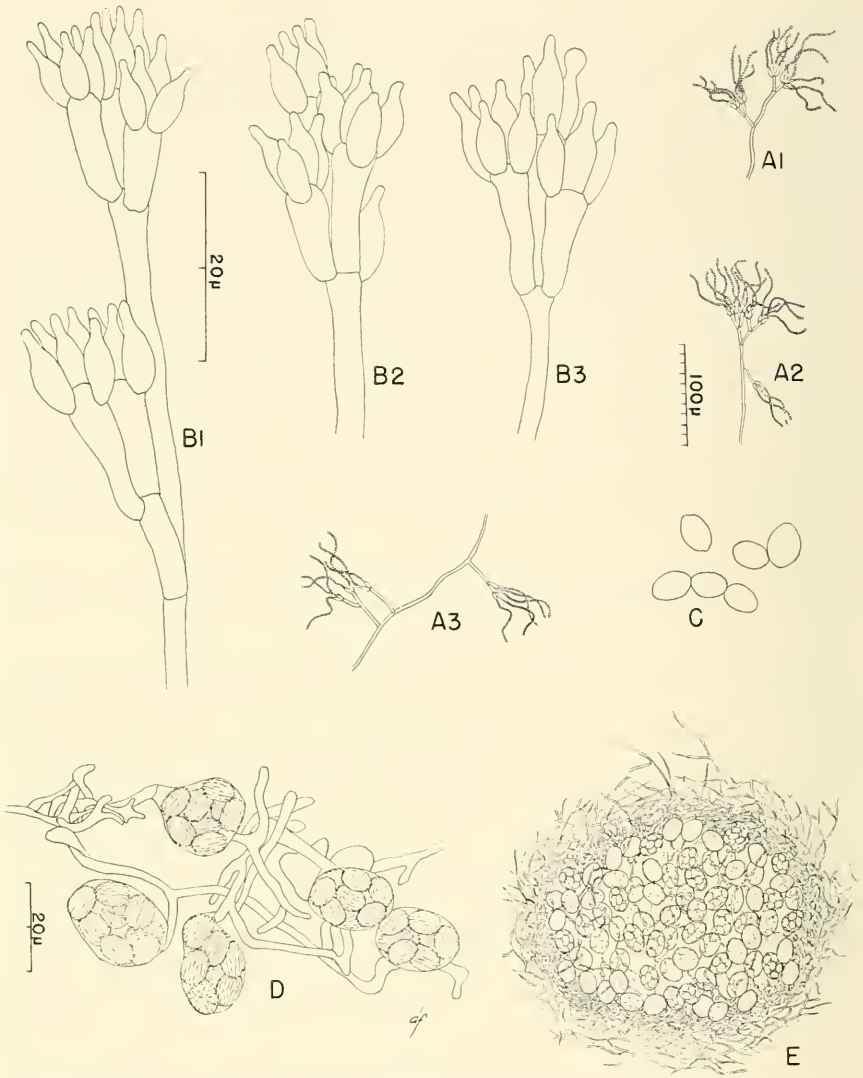


FIG. 156. *Penicillium striatum* Raper and Fennell. A_1–A_3, Habit sketches of representative penicilli. B_1–B_3, Camera lucida drawings of individual penicilli showing the diversity of pattern encountered. *C*, Mature conidia. *D*, Fertile hyphae bearing asci terminally on short branches. *E*, Diagrammatic representation of a cross section through a perithecium, × 150. Neither the pattern of the penicillus nor the sterigmata are typical of the Biverticillata-Symmetrica, but the character of its perithecia places *P. levitum* in the *P. luteum* series more satisfactorily than elsewhere.

extending the entire length of the spore, and tending to converge at the two ends.

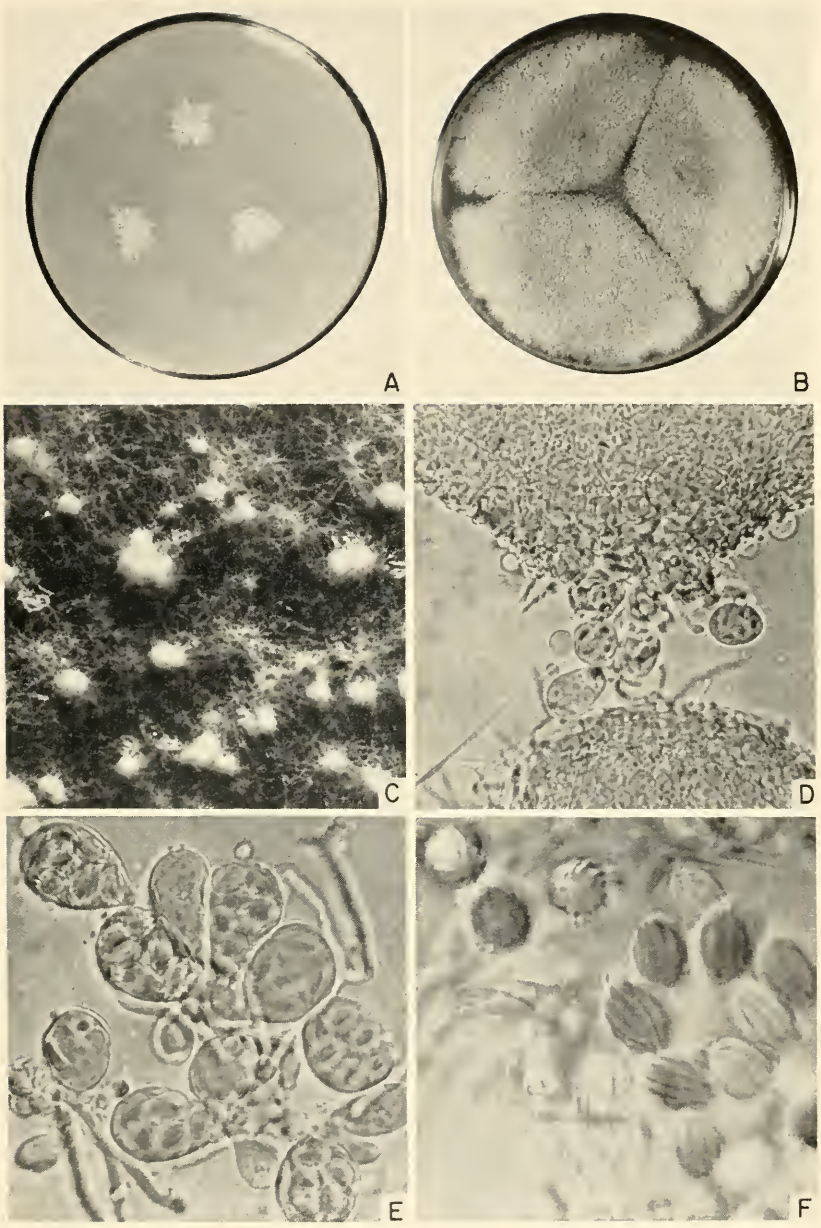


FIG. 157. *Penicillium striatum* Raper and Fennell, NRRL 717. *A* and *B*, Two-week-old colonies on Czapek and malt agars. *C*, Perithecia as seen on corn meal agar, × 30. *D*, Crushed perithecium with asci escaping through the loose hyphal envelope which bounds the perithecium, × 450. *E*, Asci in various stages of development showing their terminal origin on short branches from the fertile hyphae, × 900. *F*, Ripe ascospores showing the prominent longitudinal frills which characterize this species, × 1500.

Colonies on steep agar growing more rapidly, attaining a diameter of 3.5 to 4.5 cm. in 2 weeks at room temperature, with margins more regular than above, often entire, with surface appearing slightly granular from abundant perithecia or almost velvety where these become confluent, at first white, becoming buff to light brown in central areas in age; exudate very limited, clear; reverse in dull to reddish brown shades; penicilli very limited in number; perithecia very abundant, often forming a continuous layer; ascospore development and measurement as above.

Colonies on malt agar spreading broadly, attaining a diameter of 6.0 to 7.0 cm. in 2 weeks, thin, plane (fig. 157B), conspicuously granular in appearance with perithecia in a dense layer at the agar surface and surrounded by a thin loose network of vegetative hyphae; reverse ranging from dull brown to purple; penicilli sparsely produced; perithecia ripening within 10 days.

Colonies on 20 per cent sucrose-Czapek agar thin-growing, restricted as on standard Czapek but producing penicilli in limited numbers but more abundantly than on the above media; penicilli irregular in pattern and complexity (fig. 156A and B), commonly monoverticillate but often developing as biverticillate structures without consistent arrangement of parts; conidiophores mostly short, 50μ or less, borne as branches from aerial hyphae, occasionally arising from the substratum and 100μ or more in length, smooth-walled, about 3.0μ in diameter; penicilli simple, monoverticillate and usually consisting of a terminal verticil of 3 to 5 or 6 sterigmata (fig. 156A_3), or biverticillate with 2 or more metulae or branches arising at a single or different levels (fig. 156B), 8 to 10μ or more in length by 3.0 to 3.5μ in diameter, occasionally almost ramigenous consisting of a number of short divergent, irregularly arranged branches bearing sterigmata; sterigmata variable in form and dimensions but mostly 8 to 10μ by 2.5 to 3.0μ with conidium-bearing tips short and definitely narrowed; conidia quickly deciduous, elliptical, mostly 3.0 to 4.0μ by 2.5 to 3.0μ, with ends usually somewhat pointed, walls smooth and comparatively heavy.

Species description centered upon a culture, now maintained as NRRL 717, isolated in 1938 by Williams, Cameron, and Williams (1941) from canned blueberries. A second strain, NRRL 2080, was isolated in January 1946 from a sample of soil from Sweden sent to us by Professor Edy Velander. This latter culture differs from the above only in producing colonies slightly more restricted and ascospores with flanges less consistently parallel. A third strain similar to the second was isolated from Swedish soil but was not retained.

The proper placement of *Penicillium striatum* remains in doubt. The general characteristics of its perithecia are strongly suggestive of the genus

Gymnoascus; and among the ascosporic Penicillia, they are most nearly approximated in *P. wortmanni* and allied members of the *P. luteum* series. The ascospores are unusually large, and show a unique type of ornamentation. Conidial structures vary in complexity from strictly monoverticillate, composed of terminal verticils of sterigmata numbering up to 5 or 6 or occasionally more, to variously branched and biverticillate, but never show either the characteristic symmetric pattern of the *P. luteum* series or the long tapered sterigmata that characterize the whole Biverticillata-Symmetrica section. Despite the basic differences shown by its conidial stage, the species is tentatively placed in the *P. luteum* series with other species producing perithecia without walls of definitely specialized cells. More exact placement must await a thorough and detailed examination of the developmental history of the species, or the isolation of additional strains transitional between it and other well defined species. For the convenience of the user of the Manual, the species is keyed with the ascosporic species of the Monoverticillata as well as members of the Biverticillata-Symmetrica that produce perithecia without definite cellular walls.

Occurrence and Significance

Members of the *Penicillium luteum* series are principally of soil origin but also occur upon many organic materials undergoing slow aerobic decomposition. Some species, notably *P. vermiculatum* Dangeard and *P. wortmanni* Klöcker, appear to be especially abundant in nature and in our experience have been obtained from sources world-wide in origin. They were commonly encountered among the molds isolated from military equipment, including canvas and other fabrics, optical instruments, leather goods, etc. undergoing deterioration in tropical and subtropical areas. Other species such as *P. avellaneum* Thom and Turesson, *P. spiculisporum* Lehman, and *P. stipitatum* Thom, occur less frequently but are apparently similarly distributed. A few species, such as *P. bacillosporum* Swift, *P. helicum* Raper and Fennell, and *P. rotundum* of the same authors, are known only as the type strains. *Penicillium luteum* Zukal in its typical form is apparently rare, for it appears to have been isolated only three or four times since Zukal described it about sixty years ago. *Penicillium striatum* Raper and Fennell was first isolated from canned blueberries, but it has since been obtained from soil also. The latter is believed to represent its natural habitat.

The name *Penicillium luteum* has been used rather loosely to include various members of the Biverticillata-Symmetrica which produce colonies showing considerable yellow mycelium, with or without attendant perithecium formation. Hence, it is frequently impossible to know the true

identity of cultures referred to in the literature under this name. We can be reasonably certain, however, that reference is made to some member of the Biverticillata-Symmetrica section.

"*Penicillium luteum*" is commonly cited as a constituent of mold populations implicated in deterioration processes. Ruschmann and Bartram (1940) reported *P. luteum* to be one of several molds causing a spoilage of flax fibres and linen yarn in Germany. Ciferri (1931) reported the species to be fairly common on dry fermented and unfermented cacao beans in the Dominican Republic. Plank (1929) reported a fungus belonging to the *P. luteum* group to occur in the larvae of the sugar cane stalkborer in Cuba, but obtained no evidence that it might be used for control of the insect. Thom and Humfeld (1932) reported non-ascosporic strains of *P. luteum* to represent the most abundant soil fungi associated with maize roots in alkaline soils. Thom and Morrow (1937) reported similar forms to be capable of decomposing organic soil residues, commonly referred to as "humus", *in vitro*.

Lipman (1937) reported *Penicillium luteum* to grow normally after a 48 hour exposure to liquid air temperatures.

Niethammer (1940) reported auxins extracted from the mycelium of *Penicillium luteum* to cause a breaking of dormancy when applied to the buds of *Syringa vulgaris*.

Penicillium striatum was found to be associated with the spoilage of canned blueberries by Williams, Cameron, and Williams (1941). The fruit had been heated to 200°F. to kill yeasts, molds, and non-sporulating, acid-tolerant bacteria. The mold occurred in enamel lined cans showing a vacuum of 12 to 15 inches, but growth was not observed in plain metal cans, apparently due to the rapid removal of oxygen by the exposed metal surfaces. The strain upon which the species was based was unusually heat resistant and capable of growing as a facultative anaerobe. The species is believed to represent a normal constituent of highly acid peat soils.

A number of biochemical studies have been based upon members of the *Penicillium luteum* series. Raistrick and Rintoul (1931), investigating the metabolic products of a culture received from the Centraalbureau as *P. luteum* Zukal (non-ascosporic strain), reported the production from glucose of a mucilagenous, laevorotatory material which they termed luteic acid. Upon mild alkaline hydrolysis luteic acid gave rise to a neutral laevorotatory polysaccharide designated luteose. Upon acid hydrolysis, this in turn gave glucose as the sole product of hydrolysis. Investigating the culture further, Birkinshaw and Raistrick (1933) found that it could elaborate luteic acid from fructose, galactose, mannose, xylose, arabinose, and glycerol as well as from glucose. Upon acid hydrolysis luteic acid gave as products malonic acid and glucose. This was considered as proof of the

conversion by this organism of the hexoses, fructose, galactose and mannose, and the pentoses, xylose, and arabinose into glucose. In this paper it was stated that their culture of *P. luteum* (Catalogue No. Ad 30) was Thom's No. 11—a strain which we now recognize as representing a non-ascosporic strain of *P. vermiculatum* (see p. 583). Subsequent to this, Anderson and Raistrick (1936) reported the same strain of *P. luteum*, when grown on a medium containing glucose as the sole source of carbon, to produce mainly luteic acid, but to form in addition a malonyl-polyglucose and small amounts of other laevorotatory polysaccharides built up of mannose, galactose, and fructose units in proportions varying with the age of the culture. In a fourth paper Anderson, *et al.* (1939) elucidated the molecular constitution of luteose, the neutral polysaccharide produced by the elimination of malonic acid from luteic acid.

The metabolic products of *Penicillium spiculisporum* Lehman were investigated by Clutterbuck, Raistrick, and Rintoul (1931) who reported the production of a new polybasic fatty acid, $C_{17}H_{28}O_6$, representing the lactone of γ-hydroxy-$\beta\delta$-dicarboxypentadecoic acid, and described its preparation, properties, derivatives, and breakdown products. This acid was subsequently named spiculisporic acid by Birkinshaw and Raistrick (1934). In addition, *P. spiculisporum* also produced succinic acid and γ-ketopentadecoic acid. The constitution of spiculisporic acid was further investigated by Asano and Kameda in 1941.

Birkinshaw, Chambers, and Raistrick, in 1942, reported the production of a new metabolic product, stipitatic acid, $C_8H_6O_5$ by *Penicillium stipitatum* Thom. The acid forms cream colored needles, melts with decomposition at 302–304°C., and is optically inactive. The acid gives a deep red $FeCl_3$ reaction whereas solutions of the disodium salt are deep yellow in color. The acid was believed to belong to a new class of mold metabolic products, except for possible relationship to puberulic acid, produced by *P. puberulum* Bainier (see p. 506). Derivatives and break-down products were described but the molecular constitution of the acid was not established. Dewar has subsequently (1945) published on its structure.

Penicillium duclauxi Series

Outstanding Characters

Colonies producing abundant coremia on all substrata, particularly steep and malt agars; variously colored, with areas of vegetative growth in yellow to orange or red shades from the presence of pigmented and encrusted hyphae, and with conidial areas dark yellow-green; reverse in orange-red, deep red, or dark brown shades.

Coremia commonly 2–4 mm. high, occasionally more, with stalks yellowish, commonly bearing conidial structures over the upper half.

Penicilli typically biverticillate and symmetrical; occasionally appearing asymmetric or fractional.
Sterigmata lanceolate in pattern, characteristic of the section.

The series is represented by a single well-marked species, *Penicillium duclauxi* Delacroix. Superficially, this fungus is suggestive of *P. clavigerum* Demelius, a strongly coremiform member of the Fasciculata. It is easily differentiated from the latter, however, by the character of its penicilli, the presence of abundant yellow to orange-red pigmented hyphae, and the production of deep orange to red colors in reverse.

Recognition of a separate series is based upon the unique cultural characteristics of the species which typifies it.

Penicillium duclauxi Delacroix, in Bul. Soc. Myc. France **8:** 107, Pl. VII. 1891. Thom, U. S. D. A., Bur. Anim. Ind., Bul. 118, p. 42, fig. 9. 1910; also The Penicillia, pp. 458–459, figs. 72 and 73. 1930.

Colonies on Czapek's solution agar growing rather slowly, attaining a diameter of 2 to 3 cm. in 12 to 14 days at room temperature, consisting of a fairly tough basal felt from which arise abundant fascicles (fig. 158A), mostly as true coremia 1–2 mm. high, but frequently as irregular tufts or masses of funiculose hyphae, often more or less zonate, variable in color, often predominantly in light yellow-green to flesh or reddish shades from the development of abundant masses and tufts of encrusted vegetative mycelium, sporulating irregularly, conidial areas in yellow-green shades near Andover green to slate olive (Ridgway, Pl. XLVII); exudate lacking to fairly abundant, in dull yellow to light brown shades; odor limited, suggesting mushrooms; reverse variously colored, at first yellow, then orange-red to deep red or brownish black shades, with surrounding agar similarly colored in lighter shades; conidiophores arising primarily from coremia or tufts of aerial hyphae (fig. 158C), less commonly directly from the substratum, variable in length up to 200 to 300μ by 2.5 to 3.0μ when arising from the substratum, or 1 mm. or more when aggregated into coremia, with walls ranging from smooth to definitely roughened; penicilli typically biverticillate and symmetrical (fig. 158D), consisting of a single terminal verticil of metulae, often fragmentary, not infrequently branched and appearing more or less one-sided, but with sterigmata in all cases showing the typical lanceolate pattern of the group; metulae usually in verticils of 2 to 5 measuring 8 to 10μ by 2.5 to 3.0μ, sometimes rebranched below the level of the sterigmatic cells; sterigmata closely parallel, 3 to 6 in the verticil, mostly 8 to 12μ by 2.0 to 2.5μ; conidia elliptical to subglobose, heavy-walled, often somewhat roughened in a more or less spiral pattern, borne in tangled chains 50 to 75μ in length.

Colonies on steep agar growing somewhat more rapidly, 3 to 4 cm. in

12 to 14 days, in some strains approximating the colonies on Czapek in texture and pattern but usually somewhat deeper and showing an increased reddish coloration, often in vinaceous fawn shades (R., Pl. XL), in others

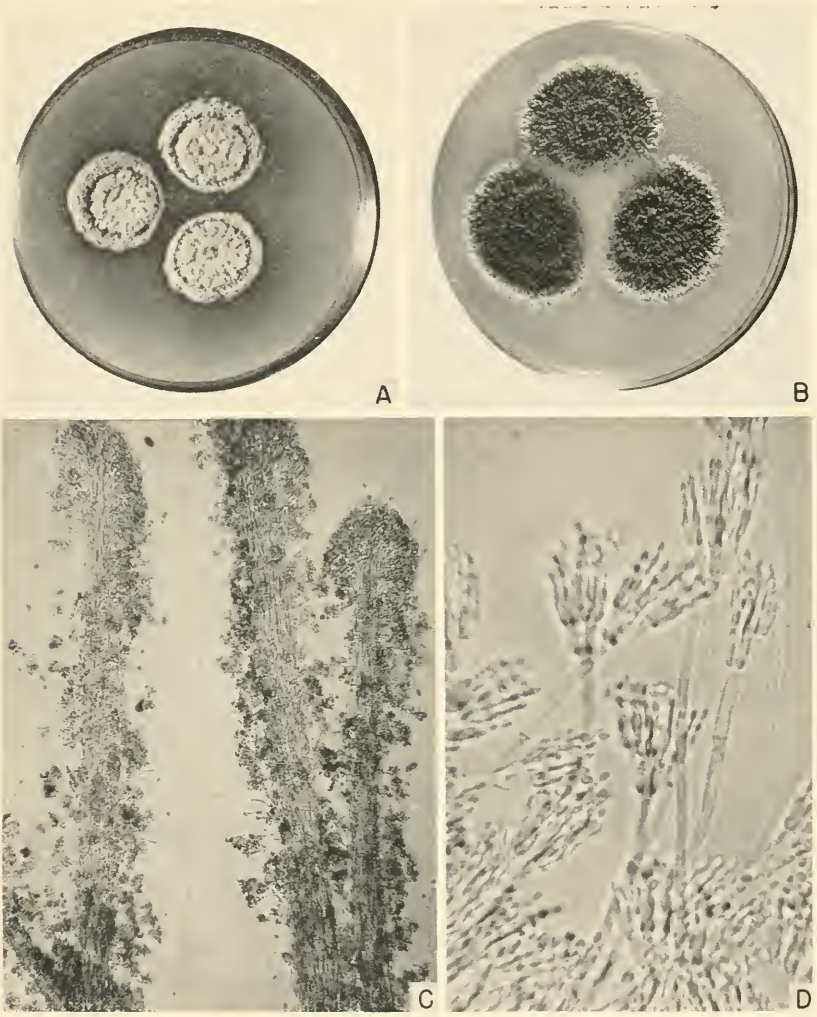


FIG. 158. *Penicillium duclauxi* Delacroix, NRRL 2020. *A* and *B*, Ten-day-old colonies on Czapek and steep agar, respectively. *C*, Coremia showing detail of structure, × 55. *D*, Enlarged view of penicilli, × 550.

consisting of a compact basal felt from which coremia 2 to 3 mm. high develop in a dense stand, coremia heavily sporing over the upper one-half with stalks appearing somewhat yellowish, colony surface in yellow-green shades

near lily green becoming deep slate olive (R., Pl. XLVII) in age; exudate limited; odor fairly pronounced, earthy; reverse in fairly bright reddish brown shades, becoming walnut to deep brown in age; penicilli more consistently symmetrical than on Czapek, with metulae and sterigmata appearing thinner and averaging more in the verticil, conidia more consistently elliptical but otherwise the same.

Colonies on malt agar growing rapidly, 5 to 6 cm. in 2 weeks, in some strains consisting mostly of tufted sterile hyphae with limited conidial development in more or less well defined zones and with conidial structures arising mostly from the substratum, in other strains producing abundant conidial structures in a velvety layer adjacent to the substratum through which subsequently develop abundant and often crowded coremia up to 6 mm. or more in length (fig. 158B) that bear conidial heads over the upper half and often appear somewhat feathery under low magnifications with stalks definitely yellowish, commonly zonately arranged, odor lacking or indefinite; reverse in dull brown to drab shades; penicilli essentially as on Czapek but commonly borne upon much longer conidiophores and showing more numerous metulae and sterigmata.

Species description centered upon Thom's notes on a strain (his No. 20) received from the author, Georges Delacroix, Paris, but now lost from the collection; NRRL 1030 received from the Thom Collection as his No. 4733.53, from Biourge in 1924; NRRL 1031, from J. W. Bowen, Johannesburg, South Africa, in 1938, as an unidentified culture; and a strain received from the Centraalbureau under this name in February 1946. The species is also represented by NRRL 2020 received in January 1946, from W. Lawrence White, Philadelphia Quartermaster Depot, as an unidentified *Penicillium* isolated from deteriorating tentage in New Guinea; and by a strain received from the Centraalbureau in February 1946, as *P. clavigerum* Demelius, which had been isolated by them in 1939 from canvas.

NRRL 1030 and the strain received from Baarn as *Penicillium duclauxi* are derived from the same source and probably represent type material. Thom received his culture (No. 4733.53) from Biourge, as the latter's No. 351. Biourge reported this as having been obtained from Dierckx who had received it from Delacroix. The strain from Baarn was contributed by Thom in 1938.

This species, in its typical form, is clearly distinct, although it is questionable whether a sharp line of separation can be drawn between it and *Penicillium clavigerum* Demelius, which we have placed in the Fasciculata along with *P. claviforme* Bainier. The two species are placed in different sections primarily upon the basis of the type of penicillus usually produced. It should be noted, however, that some penicilli in *P. clavigerum* consist of a single terminal verticil of metulae and strongly suggest the Biverticillata-

Symmetrica. Conversely, some penicilli in *P. duclauxi* are branched and asymmetrical, hence suggest the pattern regarded as characteristic of *P. clavigerum*. In describing the latter species Demelius (1923) called attention to the yellow stalks of the coremia, and it is possible that in her description and figures the prevailing pattern of the penicillus was misinterpreted. It is likewise possible that she may have been dealing with a strain somewhat transitional between the two species as they are understood by us. Until the relationship of the two species can be clarified by the isolation and examination of additional strains, we believe that the user of the Manual will benefit by the separation here proposed.

A culture received from the Centraalbureau in March 1946, as *Penicillium granulatum* Bainier from Ciferri in 1933, deserves special consideration. This strain, maintained by us as NRRL 2151, produces rapidly spreading colonies with conspicuous coremia up to 4 mm. high arranged in more or less well-defined zones in central to subcentral colony areas. Colonies are characterized by the production of an abundant, heavily encrusted, yellow mycelium and dark yellow green conidial areas as seen in many of the Biverticillata-Symmetrica. Furthermore, conidia are comparatively heavy-walled and strongly elliptical as in many members of this Section. It differs from typical members of the section, however, by producing biverticillate penicilli that are characteristically irregular in pattern, although an occasional structure appears more or less symmetrical. Walls of conidiophores and cellular elements of the penicilli are entirely smooth. Unlike most members of the section, no red pigmentation has been observed on any substratum tested. Its obvious affinities, except for the pattern of its penicilli, appear to be with *P. duclauxi* Delacroix, although the culture does not conform closely enough to be considered a member of this species. Should other strains approximating the above be encountered, recognition of an additional species in the *P. duclauxi* series should be seriously considered. Under no consideration can the culture be regarded as representing *P. granulatum* Bainier which is lacking in yellow color, and which produces large biverticillate, asymmetrical and conspicuously roughened penicilli that are entirely characteristic of the Fasciculata (see p. 544).

Occurrence and Significance

Penicillium duclauxi appears to be fairly abundant in nature and to be widely distributed. It is possibly significant that two of the strains cited above were isolated from deteriorating canvas. Others have come from soil and from decaying vegetation.

Borquelot and Graziani (1892) studied the physiology of the species. Dox (1910b) reported *Penicillium duclauxi* to be the best catalase producer of twenty-two species of *Penicillium* studied.

Penicillium funiculosum Series

Outstanding Characters

Colonies with surface appearing funiculose, floccose-funiculose, or somewhat tufted; usually spreading but occasionally more or less restricted; variously colored, with conidial areas usually in yellow-green shades and with aerial vegetative mycelium (often abundantly produced) in yellow to yellow-orange, buff to flesh, or pink to reddish shades; reverse usually in red, orange-brown, or reddish brown shades, but sometimes developing drab or greenish tints.

Conidiophores commonly arising from ropes or tufts of aerial hyphae, less commonly from the substratum or the basal felt; with walls smooth or slightly roughened, colored in some species and strains.

Penicilli typically biverticillate and symmetrical, usually consisting of a simple verticil of metulae but in some strains showing metulae rebranched below the level of sterigmata and in others developing mostly fractional structures.

Sterigmata lanceolate or acuminate, long-tapered, characteristic of the Biverticillata-Symmetrica.

Conidia usually elliptical, but ranging through subglobose to globose; with walls variable, from smooth to conspicuously roughened.

Odor usually lacking or not pronounced.

Series Key

1. Colonies with surface appearing funiculose, floccose-funiculose, or somewhat tufted; conidiophores arising primarily from aerial hyphae or ropes of hyphae. *P. funiculosum* series
   a. Conidial chains tangled or divergent; metulae parallel or somewhat divergent.
      1′. Colonies usually spreading broadly upon most substrata.
         aa. Conidia elliptical to fusiform smooth or nearly so; reverse in pink to deep red or orange-brown shades, occasionally almost black. *P. funiculosum* Thom
         bb. Conidia globose, conspicuously echinulate; reverse uncolored or in pale drab to greenish shades, becoming dull brown in age. *P. verruculosum* Peyronel
      2′. Colonies usually more or less restricted upon most substrata.
         aa. Conidia elliptical, heavy-walled, smooth; conidiophores uncolored; colonies bristly, showing areas of red, orange, or yellow mycelium and dark green conidia..... *P. islandicum* Sopp
         bb. Conidia ovate to elliptical, thin-walled, smooth; conidiophores heavy-walled, dull yellow-green; colonies fibrous to floccose or floccose-funiculose, mostly in buff to orange-pink shades... *P. varians* Smith
   b. Conidial chains forming a conical or pyramidal mass; metulae numerous, incurved..... *P. piceum* Raper and Fennell

Members of this series are cosmopolitan in habitat and apparently world-wide in distribution. Typically, they represent soil forms but com-

monly occur upon a variety of organic substrata subjected to air or water-borne contamination. They are frequently isolated from stored grains, forage products, improperly cured lumber, moist paper stocks, tentage, tarpaulins, and other protective fabrics exposed to weathering processes.

Many species, apparently belonging to this series, have been described by different authors. Of this number, five are recognized in the current treatment. Our selection of species may appear somewhat arbitrary, and in some cases it has had to be based upon non-authentic cultures and what we know to be inadequate descriptions. Nevertheless, we feel that a satisfactory separation can be made along the lines proposed. Where definite cultural entities have been assigned to species names, it is with the belief that such entities represent approximately the type of molds originally studied and described. Recognized species are based upon type material wherever possible, or upon names which, through common usage, have become widely accepted.

Penicillium funiculosum Thom is by far the most abundant and the most variable species belonging to the series. Included within our diagnosis of this species are, undoubtedly, cultural patterns described by other workers as separate species. Such a range of variation between strains has been encountered, however, that satisfactory lines of separation are lacking. In its typical aspect the species produces broadly-spreading, strongly funiculose, and comparatively heavily sporing colonies in which the conidial structures arise from aerial ropes of hyphae, rather than from a basal mycelial felt or a submerged mycelium. Colonies show an unusually wide range of colors in areas of vegetative mycelial growth and in colony reverse.

Penicillium islandicum Sopp is probably the most distinctive member of the series. Colonies grow somewhat restrictedly upon all media, are comparatively deep, and are more or less tufted rather than conspicuously funiculose; they are usually marked by a characteristic coloration involving areas of mixed orange, red, and dark yellow-green.

Penicillium varians Smith is a strongly funiculose form which develops conidiophores of fairly unique pattern. These are regularly short and usually show heavy walls that are dull green in color. The conidiophores usually arise from short cells which simulate rather closely the foot-cells that characterize the bases of the conidiophores in the genus *Aspergillus*.

Penicillium verruculosum Peyronel is characterized particularly by its globose and conspicuously roughened spores. Colonies are broadly spreading, more or less funiculose, and generally run toward yellow-green colors —seldom, if ever, developing true reds.

Penicillium piceum Raper and Fennell is characterized by comparatively loose colonies that consist of a network of much branched, interlacing

hyphae bearing very short conidiophores. Conidial chains adhere into close, compact columns which retain their general form even in fluid mounts. The columnar nature of the spore masses results in large measure from the incurved character of the metulae. The species doubtfully belongs with the other members of this series, but we believe that it will be found here more readily than elsewhere.

Whereas strains of *Penicillium islandicum* and, we believe, *P. piceum*, are comparatively stable in laboratory culture, most of the members of this series are extremely variable and unusually inconstant. Thus it is often difficult to satisfactorily assign a given culture to some particular species. Generally, this is more annoying than serious, however, for placement in the series is usually sufficiently accurate for most studies. The funiculose character of the surface growth, together with the characteristic pattern of the conidial structure should enable the investigator to go this far without difficulty.

Penicillium funiculosum Thom, in U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, p. 69, fig. 27. 1910. The Penicillia, pp. 464–465, fig. 77. 1930.

Colonies on Czapek's solution agar spreading broadly in most strains, commonly 4.5 to 5.5 cm. in 12 to 14 days at room temperature, consisting of a fairly tough basal felt, usually with aerial growth loose-textured and varying in depth up to 2 to 3 mm., in most strains showing aerial ropes of hyphae (figs. 159A and 159C), often large and conspicuous and commonly dominating the colony appearance, in others more or less tufted, especially in central colony areas, and in still others essentially floccose with ropiness evident but strongly reduced; variable in color depending upon the relative amounts of vegetative mycelium and conidial structures and the pigmentation of the underlying agar, in some strains white to pink or flesh shades, in others developing yellow to orange or red colors with some encrustment of aerial hyphae; sporulating irregularly, often heaviest in central and marginal colony areas, conidial areas varying in color, usually in yellow-green shades from pea green through sage green to slate olive (Ridgway, Pl. XLVII) or deep grape green to Lincoln green (R., Pl. XLI), but with colors of conidial areas often altered or obscured by pigmented hyphae; exudate lacking or limited in amount, clear or lightly colored; odor lacking or mild, slightly earthy; reverse variable from flesh through pink to deep red, or in some strains orange-brown, usually deeper under areas of heaviest conidial development; conidiophores arising mainly at right angles from funiculose hyphae, often very short, in marginal areas sometimes arising directly from the substratum, ranging from 100 to 300μ long by 2.5 to 3.0

or 3.3μ in diameter, with walls smooth or nearly so, in some strains lightly colored, mostly simple but occasionally branched in the terminal area; penicilli typically biverticillate and symmetrical (fig. 159D), usually consisting of a single terminal verticil of metulae, often of different lengths (the central metula usually longest), not infrequently showing individual

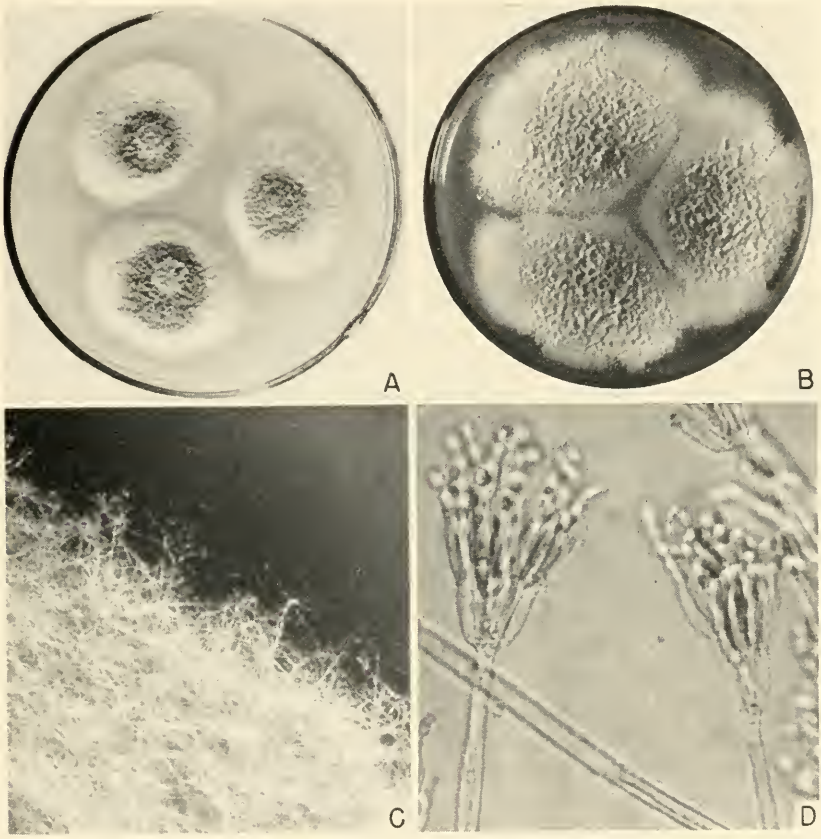


FIG. 159. *Penicillium funiculosum* Thom. *A*, NRRL 2075 growing on Czapek agar at ten days. *B*, NRRL 1032a growing on malt agar, same age. *C*, Portion of colony margin from *B* showing funiculose habit of aerial growth, × 15. *D*, Detail of typical penicilli in the same strain, × 1000.

metulae rebranched below the level of the sterigmata, with walls of metulae and sterigmata sometimes lightly colored in greenish tints; metulae mostly 5 to 8 in the verticil, about 10 to 13μ by 2.2 to 2.8μ, occasionally longer; sterigmata mostly in verticils of 5 to 7, closely parallel, about 10 to 12μ by 1.8 to 2.2μ but in individual strains often longer or shorter; conidia elliptical

to subglobose, mostly 2.5 to 3.5μ by 2.0 to 2.5μ, with walls comparatively heavy, smooth or delicately roughened, borne in tangled chains up to 100μ in length.

Colonies on steep agar essentially as on Czapek but usually heavier sporing and more conspicuously funiculose; reverse usually showing less red, commonly in orange-brown shades; conidial structures generally similar to the above in basic pattern but thinner, with individual cellular elements longer, and with walls colorless but sometimes appearing granular on the surface.

Colonies on malt agar spreading broadly (fig. 159B), with ropiness usually prominent, consistently heavier sporing, commonly dull gray-green to yellow-green near vetiver or Andover green or slate olive (R., Pl. XLVII); conidial structures as on Czapek but with cellular elements slightly longer.

Species description based on Thom's original diagnosis and our observations of numerous cultures examined in the current study. No single culture can be cited as entirely typical, since individual strains vary materially depending upon the substratum and other environmental factors. Furthermore, strains are subject to marked change under laboratory cultivation, usually becoming progressively less pigmented and less heavily sporing. The following strains, however, may be regarded as representative of the species: NRRL 1032a, isolated as an air contaminant in Washington, D. C., in July 1940, and diagnosed at the time as *Penicillium pinophilum* Hedgcock; NRRL 1033, received in 1926 from Miss A. M. Bottomley, Pretoria, South Africa, as an unidentified strain; NRRL 1768 f om C. W. Hesseltine, University of Wisconsin in 1941 as a soil isolate; NRRL 2126 from W. Lawrence White, Philadelphia Quartermaster Depot in May 1945, as an isolate from samples of mercury-treated fabric; a culture received from the Centraalbureau in March 1946, under the name *P. funiculosum* Thom (originally from Thom, 1936); and an additional culture from the Centraalbureau as *P. luteo-viride* Biourge, now maintained in our Collection as NRRL 2127.

Many strains of *Penicillium funiculosum* comply quite satisfactorily with the species description presented above. Others differ from it in one or more important characteristics, but show sufficient gradations to preclude their recognition as separate species. The following cultures may be cited as typifying recognized variations within the species, in a broad sense:

NRRL 2075 (fig. 159A), received in September 1946 from Dr. R. E. Shope, Rockefeller Institute for Medical Research, Princeton, N. J., as an isolation made originally in Guam, is characterized by the production of abundant yellow to red, sterile, encrusted hyphae. The colony reverse shows rich orange-red, brownish red, or deep blood red shades. Penicilli are commonly rebranched one or more times below the level of the sterig-

mata. The stock strain is extremely variable in culture and from it, substrains have been developed which duplicate the species description presented above. Occasional substrains are strongly suggestive of the vari-colored colonies of *Penicillium islandicum* Sopp.

NRRL 1034, received in 1926 from Miss Bottomley, Pretoria, South Africa, differs from the species proper in producing restricted colonies upon all substrata. Colonies on Czapek's agar are comparatively close-textured, sometimes produce abundant deep red exudate and show red to deep red shades in reverse; upon malt agar colonies are conspicuously tufted, funiculose, with sterile yellow mycelium abundantly evident in marginal areas, and produce a fragrant odor suggestive of *Penicillium purpurogenum;* penicilli and conidia are typical of *P. funiculosum.* A culture received from the Centraalbureau in June 1946 as *P. minio-luteum* Dierckx, isolated in 1931 from narcissus, duplicates NRRL 1034 in all essential cultural and structural characteristics.

NRRL 2118, received in March 1946 from Professor W. H. Weston, Harvard University, as an isolate from deteriorating military equipment, is characterized by floccose-funiculose colonies with abundant pinkish buff vegetative mycelium, limited yellow-green conidial areas and abundant straw-colored exudate; reverse is in orange to deep red shades; penicilli are characterized by unusually long metulae and sterigmata; conidia are smooth-walled and strongly elliptical, about 3.3 to 3.8μ by 1.8 to 2.4μ. The strain is regarded as possibly approximating the type of culture upon which the species *Penicillium pinophilum* Hedgcock was originally based (see p. 620).

NRRL 1132, isolated as a culture contaminant in Washington, D. C., in September 1940, is characterized by the production of strongly funiculose colonies with central areas up to 5 or 6 mm. deep; reverse orange-red to cherry red; conidiophores bear relatively short penicilli; walls of conidiophores, metulae, and sterigmata are comparatively heavy and definitely greenish. In older cultures on malt extract agar, this strain characteristically produces reddish brown to dark brown sclerotium-like bodies, usually embedded in the upper surface of the agar medium. Except for limited differences in color, these structures are strongly suggestive of the sclerotia that characterize *Penicillium novae-zeelandiae* van Beyma. The sclerotia differ from those of *P. purpurogenum* var. *rubri-sclerotium* Thom primarily in being produced within, rather than upon the surface of the substratum.

NRRL 1035, received in 1936 from George Smith, London School of Hygiene and Tropical Medicine, as an unidentified culture, is characterized by rapidly spreading, strongly funiculose, heavily sporing, light gray-green colonies showing little or no yellow to red colors in mycelium or reverse;

penicilli are typical of the species but produce very small elliptical to subglobose conidia measuring about 1.8 to 2.2 by 1.5μ.

NRRL 2119, received in May 1943, from Dr. Franz Lozet, Institut National pour l'Étude Agronomique du Congo Belge, differs from the species as described above in producing colonies on malt agar with marginal areas conspicuously granular from the aggregation of conidial structures into definite tufts or fascicles, occasionally appearing almost coremiform. These colonies are characterized by an aromatic odor suggesting spiced apples. In form and dimensions, the penicillus essentially duplicates that of the species *Penicillium funiculosum*. The strain is possibly transitional in the direction of *P. purpurogenum* Stoll.

Other investigators encountering members of this series have placed particular emphasis upon individual strain characteristics and have established species upon the basis of such differences. Of species that have been described we believe the following would be covered by the broad description of *Penicillium funiculosum* given above:

Penicillium pinophilum Hedgcock (in Thom, U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, pp. 37–38, fig. 6. 1910; Thom, The Penicillia, pp. 462–463, figs. 75 and 76. 1930) was isolated originally from pine wood which was strongly discolored by it—hence the name. The species was described in terms which fail to separate it from *P. funiculosum* Thom. Published illustrations likewise fail to reveal significant differences. The species is regarded as a member of the *P. funiculosum* series, probably synonymous with the species. A culture received from the Centraalbureau in July 1946, under this name as a culture from Thom in 1930, produced restricted, close-textured, and "wet" colonies on Czapek and steep agars without developing any conidial structures at 4 weeks; abundant but fragmentary penicilli with long thin sterigmata were produced on malt agar. We are compelled to regard this strain merely as a degenerate member of the *P. funiculosum* series.

Penicillium africanum Doebelt (Ann. Mykol. **7**: 315–338. 1909) was inadequately described, but is believed to have represented a member of this series. A culture, presumably Doebelt's, was received by Thom from Pribram and was observed in culture as No. 4777.5 (The Penicillia, p. 466. 1930). It represented a biverticillate form with anastomosing ropes of hyphae bearing conidiophores as short branches, and was reported to be "closely related to Thom's *P. funiculosum*." A culture from the Centraalbureau, received in February 1946, under this name, as an isolate made by van Beyma in 1928, proved to be a typical strain of *P. funiculosum*, duplicating NRRL 1033 and 1032a cited above.

Penicillium luteo-viride Biourge (Monogr., La Cellule **33**: fasc. 1, pp. 242–243; Col. Pl. VII and Pl. XI, fig. 62. 1923) was described in terms which led Thom (1930) to place it adjacent to the *P. funiculosum* series. Re-examination of Biourge's description and of notes made on a culture regarded by Thom as representative of this species fails to furnish adequate bases for separation from *P. funiculosum*, when the species is considered in a broad sense. Thom reported conidia as rough, but this character is so variable in the series as to be of doubtful significance. A culture received from Baarn under this name, and now maintained as NRRL 2127, is listed above as representative of *P. funiculosum* Thom.

Penicillium minio-luteum Dierckx (Soc. Scient. Brux. **25**: 87. 1901) was reported by Biourge (La Cellule **33**: fasc. 1, pp. 237–239; Col. Pl. VII and Pl. XII, fig. 67. 1923) in terms which led Thom (1930) to regard the species as doubtfully separable from his *P. funiculosum*. Biourge's culture confirmed this placement.

Penicillium verruculosum Peyronel, in I germi atmosferici dei funghi con micelio, p. 22, Padova. 1913. Thom, The Penicillia, p. 474. 1930.

Colonies on Czapek's solution agar growing fairly rapidly, attaining a diameter of 5.0 to 5.5 cm. in 12 to 14 days at room temperature, usually plane or nearly so but often showing a small, slightly raised central umbo, azonate, consisting of a thin and comparatively loose mycelial felt, tearing easily, surface appearing fibrous to more or less floccose-funiculose, producing abundant conidial structures primarily from the basal felt intermixed with branching aerial yellow-encrusted hyphae, mostly in bright yellow-green shades near deep sea foam green in marginal areas through chrysolite greens, becoming jade green in age (Ridgway, Pl. XXXI); exudate lacking; odor lacking or indefinite; reverse uncolored or showing pale drab to greenish shades which become dull brown in age; conidiophores mostly 75 to 100μ long by 2.2 to 2.8 or 3.0μ in diameter, smooth-walled; penicilli typically biverticillate and symmetrical, comparatively short and broad, consisting of a terminal verticil of 5 to 9 metulae, about 7 to 8μ by 3.0 to 3.5μ; sterigmata in clusters of 5 to 7, measuring 8 to 10μ by 2.2 to 2.8μ with sharply tapered conidium bearing tubes; conidia globose or nearly so, 2.8 to 3.5μ, with walls conspicuously echinulate, becoming dark green in age, borne in tangled chains up to 50μ or more in length.

Colonies on steep agar growing somewhat more rapidly, 6.5 to 7.0 cm. in 12 to 14 days at room temperature; radially furrowed, with mycelial felt as described on Czapek, producing abundant conidial structures from the loose basal felt, intermixed with yellow-encrusted hyphae, sometimes with the whole colony more or less overgrown by white sterile mycelium, growing margin wide, white to light yellow-green near sea foam to deep sea foam green (R., Pl. XXXI), becoming Lincoln green to dusky olive-green (R., Pl. XLI) with the development of mature conidial structures; exudate limited, clear, in small droplets throughout the entire colony; odor faint, slightly moldy; reverse uncolored or in slight flesh tints, developing drab to brownish olive shades in age; details of the penicilli as described on Czapek.

Colonies on malt agar 6.5 to 7.0 cm. in 12 to 14 days, plane or nearly so (fig. 160C), colony texture and color as described on Czapek except more definitely funiculose, slightly deeper and becoming somewhat darker green near yew green (R., Pl. XXI) from a more abundant production of conidial structures; exudate limited to almost lacking; odor lacking; reverse almost uncolored with only a suggestion of rose or green shades; conidiophores

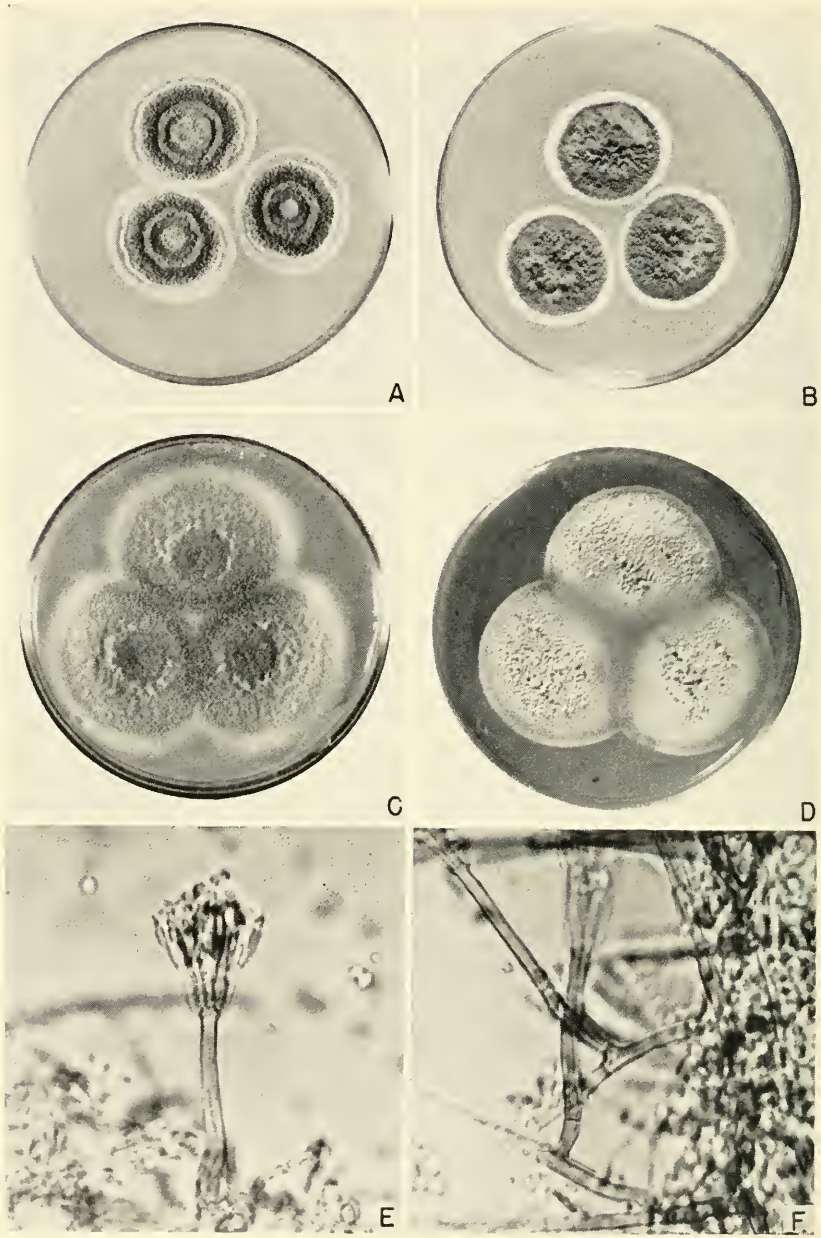


FIG. 160. *A* and *B*, *Penicillium islandicum* Sopp, NRRL 1038, ten-day-old colonies on Czapek and malt agars. *C*, *P. verruculosum* Peyronel, NRRL 1050, on malt agar at ten days. *D*, *E*, and *F*, *P. varians* Smith, NRRL 2096. *D*, Colonies on malt agar at ten days. *E*, Penicillus showing characteristic biverticillate and symmetrical pattern, × 1000. *F*, Detail of conidiophores showing heavy, dark (greenish) walls originating from hyphal elements which often simulate the foot-cells of *Aspergillus*, × 1000.

usually longer than on Czapek, up to 200 or 250μ in length; penicilli as described above.

Species description centered upon NRRL 1050, received in 1930 as a soil isolate from M. B. Morrow, University of Texas; and NRRL 2131, received from Professor William H. Weston, Harvard University, as an unidentified strain isolated from materiel exposed in Florida. The species is represented by two additional strains, also isolated in the Florida exposure tests.

Superficially, there is little cultural basis for separating this species from some of the lightly pigmented strains of *Penicillium funiculosum*. Structural details, however, differ markedly. The penicilli are shorter, wider, and relatively more compact; the metulae and sterigmata are shorter and relatively heavier; and the conidia are globose and strongly echinulate. These forms are clearly distinct from typical strains of *P. funiculosum* Thom, or any of its recognized variants and warrant recognition as a separate species. Except for the absence of columns of conidial chains, the above strains seem to agree reasonably well with Peyronel's meager description of *P. verruculosum* (isolated from air in Northern Italy), hence they are assigned to this species.

Culturally the species, as presented here, is very distinct from *Penicillium aculeatum* Raper and Fennell, but details of structure show much in common in the two species. *Penicillium verruculosum* as described above would probably have been included in Thom's "*P. luteum* series, non-ascosporic," in the broad sense that this usage was employed in his Monograph (1930), since it is characterized by rather rapidly growing colonies with a strong admixture of yellow, sterile mycelia and dark green conidial heads to give a pronounced yellow-green effect.

NRRL 2135, received from Professor W. H. Weston, as an isolate from exposed fabrics in Florida, is believed to represent an extreme variant of the species characterized by some nutrient deficiency, possibly an absence or inadequacy of invertase. It differs from the typical strains cited above primarily in producing very limited and restricted colonies on Czapek's solution and steep agars which do not exceed 2 to 3 mm. in diameter in two to three weeks. Colonies on malt agar are broadly spreading, heavily sporing, dark yellow-green, and are essentially typical of the species. Penicilli are characteristic of the species and produce globose, strongly roughened conidia.

Penicillium islandicum Sopp, in Monogr., pp. 161–164, Taf. XVII, fig. 122; Taf. XXIII, figs. 25 and 26. 1912. Thom, The Penicillia, pp. 466–467. 1930.

Colonies on Czapek's solution agar (Col. Pl. X) slow-growing, attaining a diameter of 2.5 to 3.0 or 3.5 cm. in 2 weeks at room temperature, often

conspicuously zonate (fig. 160A), lightly wrinkled in a radial pattern, variously colored in yellow-orange, orange-red, brown, and dark yellow-green shades, from irregular or interrupted production of conidial structures and pigmented hyphae, consisting of a fairly tough felt of orange to red encrusted mycelium from which arise ascending or funiculose hyphae bearing the conidiophores as short branches, with alternate zones or localized areas in which sterile hyphae or conidial structures dominate the colony surface, margins in flesh to orange shades, about 1 to 4 mm. wide, sporulating abundantly in most strains, commonly in localized zones or areas, in dark yellow-green shades through artemisia to lily green or even deep slate green in age (Ridgway, Pl. XLVII), in some strains lightly sporulating with white to orange or red mycelium predominant; exudate limited to fairly abundant, occurring mostly as microscopic beads along the hyphae, or collecting into small droplets and often becoming overgrown by secondary mycelial growth to produce a superficially nodular appearance; odor indefinite to rather sharp, difficult to characterize; reverse in orange-brown to red shades, becoming dull in age; conidiophores short, commonly 50 to 75μ, borne almost entirely as branches from ascending aerial hyphae or ropes of hyphae, occasionally from the substratum and measuring 100 to 150μ by 2.5 to 3.0μ, often appearing rough and encrusted when viewed dry, but smooth in fluid mounts; penicilli usually consisting of a compact terminal verticil of metulae, not infrequently branched but with the branches also terminating in typical biverticillate-symmetrical structures, occasionally with a secondary verticil lower down on the conidiophore; metulae 4 to 6 in the verticil, 8 to 10μ by 2.2 to 2.8μ; sterigmata parallel, closely packed, in clusters of 5 to 8, shorter and less gradually tapered than in most members of this group, 7 to 9μ by 1.8 to 2.2μ; conidia elliptical, 3.0 to 3.5μ by 2.5 to 3.0μ, heavy-walled, smooth, borne in short tangled chains.

Colonies on steep agar growing somewhat more rapidly (fig. 160B), 3.5 to 4.0 cm. in 2 weeks at room temperature, otherwise as described above; exudate lacking; odor faint, slightly fragrant; details of the penicilli as described above.

Colonies on malt extract agar 2.5 to 3.5 cm. in 2 weeks at room temperature, in most strains comparatively thin, plane, with center slightly raised, in others 2 to 3 mm. deep, loosely floccose-funiculose, with a conspicuous development of orange to orange-red encrusted mycelium in all strains, zonate, medium to heavily sporing; margins irregular; exudate lacking; odor more or less fragrant; reverse in orange to rose shades; microscopic details as described on Czapek's agar but conidia borne in loosely parallel chains up to 100μ in length.

Species description centered upon NRRL 1036, 1037, 1038, and 2115 as typical, and upon numerous other strains examined in connection with this

PLATE X

TOP: Penicillium islandicum Sopp, NRRL 2115, on Czapek's solution agar, 10 days. *CENTER: Penicillium purpurogenum* Stoll, NRRL 1061, on Czapek's solution agar, 12 days *BOTTOM: Penicillium herquei* Bainier and Sartory, NRRL 1040, on Czapek's solution agar, 10 days. (Color photographs by Haines, Northern Regional Research Laboratory. Reproduced through co-operation of Chas. Pfizer & Co., Inc.)

and earlier investigations. This species is one of the most tangible members of this section and appears to be one of the least variable. The first of the above listed cultures was received in 1922 from Putterill, Cape Town, South Africa, and was discussed by Thom in his Monograph as representative of the species (No. 4658.144.2). It has remained unchanged during the ensuing years of laboratory cultivation. Other strains, held for similar lengths of time have remained equally stable, and new isolates are commonly encountered which duplicate the above in cultural and microscopic characteristics.

This species was correctly placed in the series with *Penicillium funiculosum* by Thom in 1930. It differs from the latter species, however, in its more restricted growth, in the production of more orange-red aerial hyphae, and in the development of shorter hyphal ropes or funicles.

Sopp based his species upon a culture found on the Island of Skyr, Norway. Cultures were reported to grow best at 20° to 25°C., but continued to grow at 8°C. and at 38°C. The species grew best upon acid media and upon substrates rich in starch. Conidia remained viable more than three years.

The species appears to be very abundant and widespread in nature and may be regarded as representing a normal member of the mycoflora of almost all soils. It was encountered several times among molds isolated from deteriorating military equipment.

Penicillium varians Smith, in Brit. Mycol. Soc. Trans. **18:** 89–90; Pl. IV, fig. 3. 1933.

Author's diagnosis as follows:

"Colonies growing moderately well on all usual media at temperatures up to 37°C.; on wort agar slightly floccose, bluish green rapidly becoming greyish green then grey, in age covered with sterile mycelium, dirty white, often with patches of pink or yellow; on Czapek agar slightly floccose or funiculose with irregular production of conidial areas bluish green, turning grey, sometimes with basal felt of gelatinous masses of hyphae, pale brown to orange-brown; reverse variously colourless spotted with faint purple or, in cultures exposed to light, definitely coloured brownish orange; conidiophores arising as short branches from interlacing hyphae or definite ropes of hyphae, articulate, slightly roughened, definitely coloured pale yellowish brown but not dematiaceous, 40–50μ by 2–2.8μ; penicilli symmetrically biverticillate; metulae 10–14μ, occasionally longer, by 2–2.5μ; sterigmata closely packed, acuminate, 10–15μ by 2μ; conidia ovate or pyriform, smooth, 3–4μ by 1.5–2.0μ."

The type strain was isolated as a single colony on a plate from a sample of cotton yarn showing no sign of mildew, and was regarded as a part of the "latent infection" of the sample. The species is known only as the type.

Our notes follow:

Colonies on Czapek's solution agar growing rather restrictedly, about

2.0 to 2.5 cm. in 2 weeks, more or less zonate and lightly furrowed in a radial pattern, with surface appearing more or less fibrous to floccose, tearing easily, predominantly in buff to orange-pink shades, light sporing in dull gray-green shades usually affecting the colony appearance only in central areas; exudate lacking; odor evident, difficult to characterize; reverse variously colored in greenish gray to dark gray shades or at times orange-red shades near salmon or apricot buff (Ridgway, Pl. XIV) in a broad marginal zone; conidiophores arising as short perpendicular branches from aerial hyphae or ropes of hyphae mostly 30 to 50μ by 2.5 to 3.0μ septate, with walls comparatively heavy and colored in dull yellow-green shades, smooth or slightly rough, sometimes arising from short cells suggesting the foot-cells of *Aspergillus* (fig. 160F); penicilli typically biverticillate and symmetrical as described and illustrated by Smith (fig. 160E) but in our cultures commonly fractional, ranging from monoverticillate through asymmetric structures with 2 or 3 metulae to occasional larger and symmetrical penicilli, metulae 8 to 10μ by 1.8 to 2.2μ with walls colored as the conidiophores; sterigmata mostly in verticils of 4 to 6, about 8 to 10μ by 1.5 to 2.0μ, lanceolate with conidium-bearing tubes characteristically tapered; conidia ovate to elliptical, up to 3.0 to 3.5μ by 2.0 to 2.5μ, thin-walled, smooth.

Colonies on steep agar somewhat larger than on Czapek but similar in pattern and texture; reverse in shades listed above; penicilli averaging slightly larger than above but otherwise similar in pattern.

Colonies on malt agar spreading broadly (fig. 160D), up to 6 cm. in 2 weeks, seldom furrowed, consisting of a fairly loose, floccose to funiculose mycelial felt, up to 1 mm. deep, lightly sporulating throughout, in light gray-green shades near mineral gray (R., Pl. XLVII); exudate lacking; odor indefinite; reverse in dirty yellow-orange to almost black shades; conidial structures as described on Czapek; metulae and sterigmata consistently longer and thinner, usually closely parallel; conidia strongly elliptical to almost cylindrical, about 2.5 to 3.0μ by 1.5 to 2.0μ.

The type strain, received from the National Collection of Type Cultures as George Smith's culture No. 91, is maintained in our Collection as NRRL 2096. The same culture received from the Centraalbureau duplicates this completely.

This unique species has apparently been isolated only once. Its funiculose habit described and illustrated by Smith and observed in all of our cultures, unmistakably placed it in the *Penicillium funiculosum* series. It differs markedly from other members of the series in the production of unusually short, conspicuously septate conidiophores with strongly pigmented walls arising from aerial hyphae usually colored in somewhat lighter shades. The type culture has apparently changed markedly during the period of laboratory cultivation. Smith originally figured it as pro-

ducing large, compact, biverticillately symmetrical penicilli (see his fig. 3, Pl. IV). Such structures are occasionally observed in our cultures but represent the exception rather than the rule. It is possible that the cul-

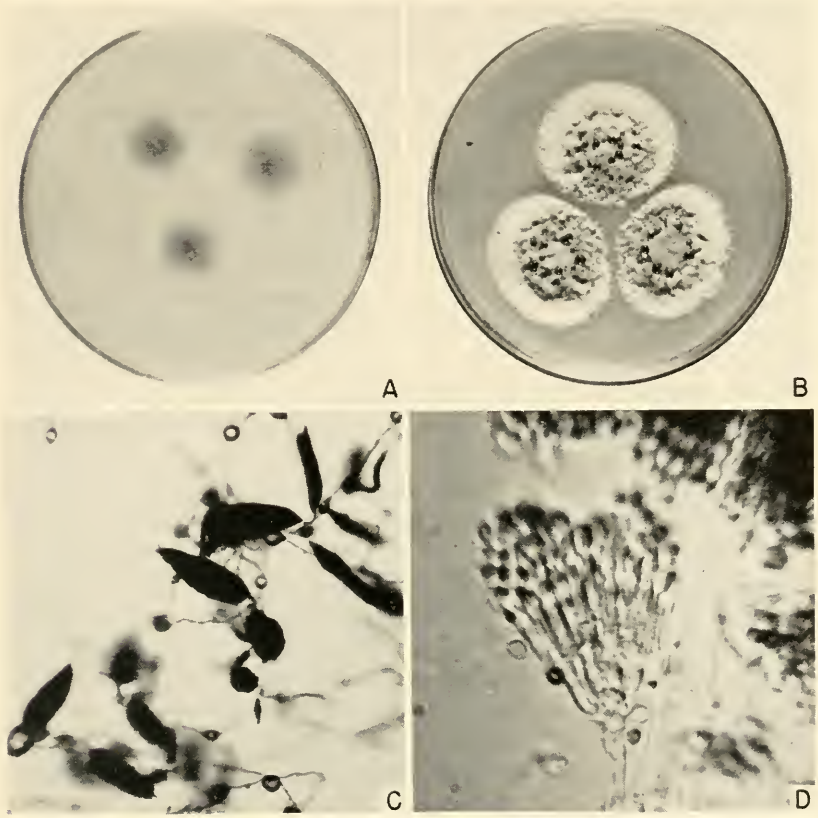


FIG. 161. *Penicillium piceum* Raper and Fennell. *A* and *B*, Ten-day-old colonies of NRRL 1071 on Czapek and malt agars. *C*, Conidial heads as seen under low power presenting the spruce-tree-like pattern that is characteristic of this species, and from which the name was taken, × 115. *D*, Penicillus showing typically crowded metulae and sterigmata, × 1000.

ture is undergoing progressive degeneration similar to that reported for the type of *P. purpurogenum* var. *rubri-sclerotium* Thom (see p. 637).

Penicillium piceum Raper and Fennell, in Mycologia, **40**: 533–535, fig. 9. 1948.

Colonies on Czapek's solution agar growing somewhat restrictedly (fig. 161A), attaining a diameter of 3.0 to 3.5 cm. in 12 to 14 days at room temperature, consisting primarily of a thin, white to yellow mycelial felt tear-

ing easily, with central area 1.0 to 1.5 cm. in diameter, raised, bearing few conidial heads but surrounded by a thinner plane marginal zone producing abundant conidial structures in a loose mycelial network, in dull yellow-green shades near tea green or pea green (Ridgway, Pl. XLVII), occasional strains lacking the prominent thin margins, but showing the entire colony area felted, producing limited numbers of conidial structures and considerable sterile mycelium throughout; exudate fairly abundant, mostly as microscopic droplets adherent to the mycelium; odor distinct, rather pleasant; reverse in brownish orange shades, with the green of conidial areas showing through in marginal areas; conidiophores arising from a loose network of short, much-branched aerial hyphae, usually about 20 to 35μ by 2.5 to 3.0μ, rarely 50μ or more, smooth-walled; penicilli very compact, typically biverticillate and symmetrical (fig. 161D), consisting of 10 to 12 metulae borne on the terminal portion of the vesicular apices of the conidiophores; metulae 8 to 10μ by 1.8 to 2.2μ, with outer metulae incurved, tending to become parallel with the main axis of the conidiophores; sterigmata typical, acuminate, parallel, occurring in crowded clusters of 5 to 7, 8 to 9μ by 1.5 to 1.8μ, producing conidia in closely adherent chains which consistently produce conical to pyramidial masses up to 150μ long (fig. 161C); conidia subglobose to elliptical, 2.5 to 3.0μ by 2.2 to 2.8μ, smooth when young, becoming heavy-walled and irregularly roughened when mature, dark olive green in mass, chains adherent and the masses of conidia retaining their conical shape even in liquid mounts.

Colonies on steep agar rapidly growing, 5.0 to 5.5 cm. in 12 to 14 days at room temperature, plane, velvety in appearance but consisting of a loose network of dwarfed aerial hyphae, heavily sporing throughout in dull yellow-green shades near slate olive (R., Pl. XLVII), surface of colonies overgrown to a greater or lesser degree by sterile encrusted yellow mycelium, becoming conspicuous in some strains; exudate limited to abundant, in small droplets, clear to very light yellow; odor as on Czapek; reverse in orange or red-brown shades becoming almost black in older areas; details of penicilli as described on Czapek, but with masses of conidia less conspicuously cone-shaped and up to 200μ in length.

Colonies on malt extract agar 4.5 to 5.0 cm. in diameter in 12 to 14 days (fig. 161B), 1 to 2 mm. deep, surface uneven from irregular tufts of funiculose encrusted hyphae, fairly heavily sporing, in yellow-green shades near vetiver to Andover green (R., Pl. XLVII); exudate limited in amount, evaporating to leave pits in the colony surface; odor fragrant, faintly suggestive of apples; reverse uncolored or showing very slight orange tints; microscopic details as on Czapek.

Species description centered upon NRRL 1051 from the Thom Collection as an unidentified culture. Duplicated by NRRL 1071 received in 1937

from C. W. Emmons, National Institute of Health, as an unidentified *Penicillium;* and NRRL 2112, received in 1945 from J. W. Groves, Ottawa, Canada as an unidentified *Penicillium* isolated from alfalfa seed.

Careful consideration of described species of *Penicillium* failed to reveal one which adequately characterized the above strains. Raper and Fennell (1948), therefore, regarded the cultures in question as representing a new species, to which they applied the binomial *Penicillium piceum* because of the striking resemblance of the typical columnar head to a compact spruce-like evergreen in miniature.

Occurrence and Significance

Penicillium funiculosum Thom is one of the most common of all soil fungi and is apparently world-wide in distribution. It has been sent to us for identification by collaborators from all parts of the United States and from many foreign countries. In our own studies it has occurred in all soils examined, irrespective of their origin. The species grows upon a variety of vegetation in the later stages of decay. It frequently occurs upon freshly sawed or moist lumber where it may produce some discoloration. It has been repeatedly encountered among cultures isolated from deteriorating military equipment submitted to us for identification. Other members of the series are less abundant in nature but in the main, are similarly distributed.

Cultures of *Penicillium funiculosum* as isolated from nature are often strongly pigmented. While the pigmentation of this and other species of the Biverticillata-Symmetrica has not attracted the attention that one might expect, it has received limited study. Ebling (1938) investigated the effect of light upon pigment production in cultures grown on malt agar slants. Cultures were reported to become strongly pigmented in light, but to become colorless with continued recultivation in darkness. The blue end of the visible spectrum was found to have the greatest pigment stimulating effect. Igarasi (1939a) studied the chemistry of the pigment. Red mycelium produced upon koji extract was extracted with 2 per cent NaOH, acidified to produce a reddish brown precipitate which was then extracted with petroleum ether. The pigment, named funiculosin, crystallized as deep red plates, melted at 218°C., and had the empirical formula $C_{15}H_{10}O_5$. The same author (1939b) isolated malonic acid from the culture solution when koji extract was used, and identified succinic and oxalic acids when a synthetic medium containing glucose and $(NH_4)_2SO_4$ was employed.

Abbott (1923, 1926), studying various soil fungi in different soil-fertilizer mixtures *in vitro,* reported *Penicillium funiculosum* to render raw rock phosphate more readily soluble.

Clark and Scales (1916) investigated the enzymes produced by a cellulose

destroying mold from soil, identified as *Penicillium pinophilum*. Kellerman (1913) had earlier demonstrated cytase (or cellulase) production by the same species. Hubert (1929) reported *P. pinophilum* to be one of the fungi causing "sap stains" in wood and discussed various methods of prevention. Hedgcock (1906) isolated the culture upon which he established the species *P. pinophilum* from pine wood, hence the name. For the reasons given above (see p. 620), we believe *P. pinophilum* to be synonymous with the more widely accepted species, *P. funiculosum* Thom.

Birkinshaw and Raistrick (1934) investigated the metabolic products produced upon Czapek-Dox solution containing glucose by a culture received from Biourge as the type of *Penicillium minio-luteum* Dierckx (see p. 621). The metabolism solution when acidified yielded a pigmented crystalline precipitate and two colorless crystalline acids. One of these, now named spiculisporic acid, was known from an earlier investigation of *P. spiculisporum* (Clutterbuck, Raistrick, and Rintoul, 1931); the other, a dextrorotatory acid, $C_{16}H_{26}O_7$, represented a new product for which the name miniolueic acid was proposed. The latter acid crystallized from hot water as colorless needles, M.P. 171°C.

Investigating the metabolic products of *Penicillium varians*, Haworth, Raistrick, and Stacey (1935b) reported the production from glucose of a previously unknown polysaccharide which they designated varianose. The compound has the empirical formula $(C_6H_{10}O_5)_n$, is a white amorphous powder, is neutral in aqueous solution and is dextrorotatory. It reduces Fehling's solution slightly and gives no color with iodine. Upon acid hydrolysis it gives a mixture of *d*-glucose, *d*-galactose, and either *l*-altrose or *d*-idose. An abstract by the same authors had appeared earlier in Chemistry and Industry (1932).

Barber (1929) discussed the production of fat by an unidentified *Penicillium* when grown upon nutrient solutions containing glucose, sucrose, or xylose. The strain was subsequently identified by Thom as approximating *Penicillium funiculosum*. The same mixture of fats was consistently produced, and included palmitic, stearic, oleic, and α and β-linoleic acids both free and as glycerides, together with some sterols.

Penicillium purpurogenum Series

Outstanding Characters

Colonies with surface generally appearing velvety or lanose, sometimes more or less flocculent; usually somewhat restricted upon Czapek agar, commonly spreading on malt; variously colored from an admixture of strongly pigmented and often encrusted aerial hyphae, in yellow, orange,

or red shades, and massed conidial structures, deep yellow-green to gray-green in color; reverse typically in deep cherry red or purplish red shades, with the surrounding agar usually colored in similar but lighter shades.

Conidiophores commonly arising from the basal felt or from submerged hyphae in thin colony margins; with walls smooth or roughened depending upon the species and strain.

Penicilli typically biverticillate and symmetrical, usually consisting of a simple verticil of metulae, which in turn bear compact clusters of parallel or somewhat divergent sterigmata, depending upon the species and strain.

Conidia usually elliptical, but ranging through subglobose to strictly globose; with walls variable, often somewhat roughened, but ranging from smooth in some species to conspicuously echinulate in another.

Odor usually pronounced, often aromatic or fragrant, commonly suggesting apples or walnuts in cultures on malt agar.

Series Key

a. Colonies on Czapek and steep agars usually developing an intense red or purple-red pigmentation; commonly producing aromatic odors suggesting apples or walnuts on malt agar ..... *P. purpurogenum* series

1′. Colonies consistently producing deep red colors in reverse; surface usually heavy sporing and showing an evident but limited development of yellow or orange-red aerial hyphae.

aa. Conidia elliptical to subglobose; penicilli comparatively long, sterigmata closely parallel; pigmentation diffusing throughout the surrounding agar.

1″. Conidia typically roughened; colonies sometimes spreading; conidial areas in dark yellow-green shades ..... *P. purpurogenum* Stoll

aaa. Producing sclerotia, at least when newly isolated. *P. purpurogenum* var. *rubri-sclerotium* Thom

2″. Conidia smooth; colonies more restricted; conidial areas in lighter yellow-green to gray-green shades ..... *P. rubrum* Stoll

bb. Conidia globose, echinulate; penicilli comparatively short; sterigmata somewhat divergent; pigmentation seldom diffusing throughout the surrounding agar ..... *P. aculeatum* Raper and Fennell

2′. Colonies developing red-orange, yellow-orange or greenish brown rather than deep red colors in reverse; surface usually characterized by prominent areas of sterile yellow aerial mycelium ..... *P. variabile* Sopp

This series includes some of the most colorful members of the genus *Penicillium*. With the exception of a single species, *P. variabile* Sopp, all members of the series are characterized by the production of intense red or purplish red pigments on Czapek and steep agars. Pigmentation is especially pronounced in the colony reverse, but in most forms diffuses quite generally throughout the entire substratum and often colors the vegetative mycelium in similar and characteristic shades.

Members of the series represent normal constituents of the mycoflora of all soils examined, and may occur also upon a wide variety of organic substrata undergoing slow decomposition.

Several species, apparently belonging to this series, have been described and it is extremely difficult to know which of these should be accepted as valid, and which should be reduced to synonymy. Our selection of species for recognition is admittedly somewhat arbitrary, as it is in the other major series which comprise this section of the genus, and further studies may indicate a need for revision or emendation of the scheme here proposed. Based upon re-examination of original descriptions and an extensive study and comparison of cultural material, we believe that a separation similar to that proposed will prove adequate for most investigators. Four species are recognized:

Penicillium purpurogenum Stoll is the most abundant and the most variable. Typically, it is characterized by dark yellow-green conidial masses against a mycelium and substrate colored in red or purple-red shades. Spores are strongly elliptical and more or less roughened in most strains. On malt agar, colonies commonly produce an aromatic or fragrant odor suggesting apples or black walnuts.

Penicillium rubrum Stoll differs from the above in producing more restricted colonies upon most substrata and in producing conidial areas of lighter yellow to gray-green color. Pigmentation of the colonies and the underlying medium is essentially as in *P. purpurogenum*. The conidia of this species are smooth-walled and often subglobose.

Penicillium aculeatum Raper and Fennell is characterized by very restricted and comparatively deep colonies on Czapek agar. Penicilli are relatively shorter and broader than in the preceding species and conidia are strictly globose and strongly echinulate.

Penicillium variabile Sopp is characterized by a marked reduction in red pigmentation, but retains the other cultural characteristics of the series. In many strains there is an excessive development of sterile yellow mycelium which oftentimes dominates the colony appearance. Conidia are strongly elliptical and smooth-walled. The colony reverse usually shows yellow-orange to orange-brown, rather than true red shades.

Thom, in his Monograph 1930, recognized a series of strains under the name "*Penicillium luteum* series—non-ascosporic," to which he assigned forms that showed a strong admixture of yellow-encrusted aerial hyphae and dark yellow-green conidial heads, often with colonies somewhat red in reverse. It was his belief that these forms, in the main, probably represented haplonts of fertile forms which, for one reason or another, had become segregated and hence incapable of developing their complete life cycle. Gradually our interpretation of the series was broadened until it

became, in effect, a catch-all for almost any conidial member of the Biverticillata-Symmetrica which was not marked by a strong pigmentation, or the development of conspicuously funiculose, strongly restricted, or exceptionally thin colonies. While some of the strains now assigned to *P. verruculosum* Peyronel in the *P. funiculosum* series were originally assigned to Thom's non-ascosporic *P. luteum* series, the latter was represented primarily by strains which we now include in *P. variabile* Sopp and place in the *P. purpurogenum* series.

Penicillium purpurogenum Stoll, in Beitrage zur morphologischen und biolgischen Characteristik von Penicilliumarten, Wurzburg, p. 32, Taf. I, fig. 6 and Taf. III, fig. 2. 1904; see also Thom, U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, p. 36, fig. 5. 1910; Mycologia **7:** 134–142. 1915; and The Penicillia, pp. 478–479. 1930.

Colonies on Czapek's solution agar (Col. Pl. X) growing rather restrictedly, attaining a diameter of 1.5 to 2.5 cm. in 12 to 14 days at room temperature (fig. 162A and E), sometimes definitely wrinkled, zonate or azonate, consisting of a yellow to orange-red mycelial felt bearing abundant conidial structures, or of massed conidial heads arising from aerial hyphae or directly from the substratum and superficially appearing velvety, or in some strains tending to become floccose with growing margin white or yellowish from an admixture of encrusted sterile hyphae; usually heavily sporing in central and sub-central areas, in deep yellow-green shades near lily green through deep slate green to dull greenish black (Ridgway, Pl. XLVII); exudate usually limited but in some strains fairly abundant, in orange-red shades; odor indistinct or slightly moldy; reverse in deep red to dark reddish purple shades, often approximating ox blood red (R., Pl. I), with surrounding agar similarly colored in somewhat lighter shades; conidiophores arising from the substratum and measuring up to 100 to 150μ in length by 2.5 to 3.0 or 3.5μ in diameter, or as branches from aerial hyphae and much shorter, about 40 to 50μ, smooth-walled; penicilli typically biverticillate and symmetrical (fig. 162C and D), compact, usually consisting of a single verticil of 5 to 7 or 8 metulae, each terminating in a compact cluster of 4 to 6 parallel sterigmata bearing short conidial chains; metulae 10 to 14μ by 2.5 to 3.0μ; sterigmata mostly 10 to 12μ by 2.0 to 2.5μ, lanceolate in form, characteristically tapered; conidia elliptical to subglobose in some strains, sometimes more or less apiculate, mostly 3.0 to 3.5μ by 2.5 to 3.0μ with walls typically heavy and irregularly roughened, sometimes showing distinct transverse bands, but in some strains almost smooth.

Colonies on steep agar spreading broadly up to 5.5 to 6.0 cm. in 12 to 14 days at room temperature, comparatively thin, plane or lightly fur-

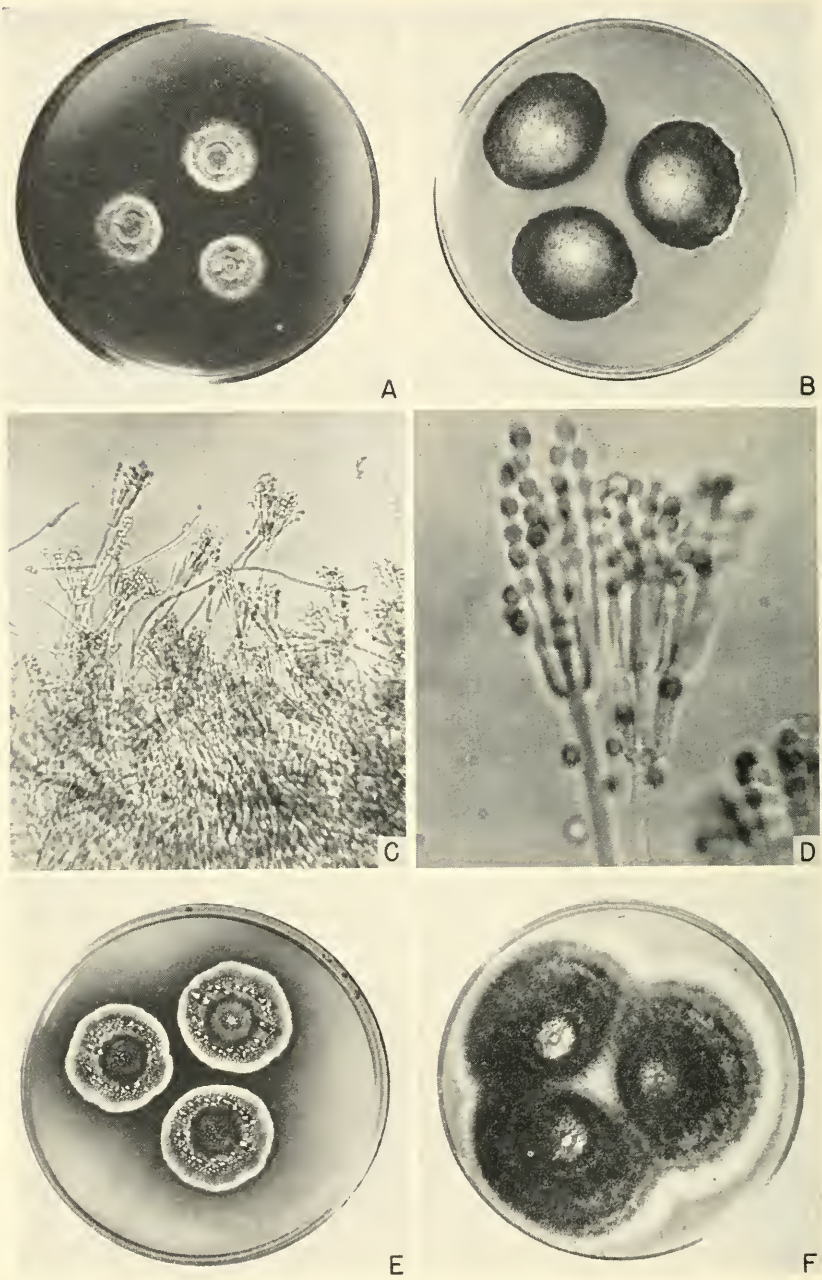


FIG. 162. *Penicillium purpurogenum* Stoll. *A* and *B*, Ten-day-old colonies of NRRL 1061 on Czapek and malt. *C*, Penicilli seen under rather low magnification, × 200. *D*, Enlarged view of penicillus, × 1000. *E* and *F*, Ten-day-old colonies of NRRL 2019 on Czapek and malt agars. Colony reverse and agar on Czapek quickly assume deep red shades as shown in *A* and *E*.

rowed, heavily sporing throughout, colored in dull to deep dark yellow-green shades often approaching slate olive in age (R., Pl. XLVII); conidiophores arising from the substratum or from trailing aerial hyphae that are conspicuously encrusted and range from yellow to orange-red in color; exudate generally lacking; odor indistinct; reverse in bright red shades ranging from deep orange-red to deep purple-red; details of conidial structures essentially as described above but with conidiophores, metulae, and sterigmata measuring slightly larger and bearing adherent or somewhat tangled chains of conidia up to 100μ in length.

Colonies on malt extract agar usually about 3.0 to 3.5 cm. in 12 to 14 days (fig. 162B and F), in some strains broadly spreading up to 5.5 to 6.0 cm., heavily sporing except in marginal areas of some strains, in dull yellow-green to deep olive shades, superficially appearing velvety but with encrusted aerial hyphae always evident and occasionally prominent, conidiophores arising mainly from the substratum, up to 200μ in length and bearing penicilli as described on Czapek but with conidial chains usually parallel or adherent in poorly defined columns up to 200μ in length; exudate lacking; odor pronounced, aromatic, suggestive of apples, in age sometimes simulating black walnuts; reverse usually uncolored or in dull yellowish brown shades.

Species description centered upon NRRL 1061 from the Thom Collection as No. 4279C, received from Dr. K. Saito, Darien, Manchuria, in 1918; duplicated also by NRRL 1136 isolated in 1940 from a mixed culture at Arlington Farm, Virginia; NRRL 1214 isolated in 1941 as a "parasite" in an *Aspergillus niger* culture used in a gluconic acid fermentation; NRRL 2019 received in April 1946, from the Philadelphia Quartermaster Depot, as an isolate made in August 1944, from deteriorating tentage collected in New Guinea; and numerous other strains essentially duplicating the above. A strain received under this name from the Centraalbureau labelled "NCTC, 1936" is probably correctly diagnosed but is somewhat atypical in producing white to flesh-colored, floccose colonies that are non-sporulating at two weeks. Colonies in reverse show the deep red colors characteristic of the species. A second strain received from the Centraalbureau as this species and labelled "Baarn, 1943" is entirely typical.

Certain individual cultures show outstanding strain characteristics, *e.g.*: some show conidia smooth or nearly so (NRRL 1147), others grow more rapidly and become almost floccose in marginal areas (NRRL 1059), others are characterized by unusually strong apple-like odors (NRRL 2019), while still others develop an abundant, yellow mycelium on malt agar (NRRL 1749). These are but a few of many variations encountered.

Penicillium purpurogenum regularly occurs in soil and decaying vegetation. It has been repeatedly isolated from moist paper stocks and starch

paste where it develops as dark green, powdery masses, surrounded by areas of bright red color. It commonly occurs upon exposed tentage and canvas, causing a marked discoloration of the fabric and sometimes producing a marked reduction in serviceability.

The following species are regarded as duplicating *Penicillium purpurogenum* Stoll:

Penicillium sanguineum Sopp (Monogr., pp. 175–176; Taf. XIX, fig. 138, Taf. XXIII, fig. 24. 1912) is believed to have been correctly assigned by Thom (1930) to the *P. purpurogenum* series. Re-examination of the original description and of Thom's notes on his culture, No. 4917.7 (now maintained as NRRL 1749), together with comparative study of this strain in culture, fails to show adequate bases for continued recognition of the species. Undoubtedly, Sopp was working with some member of the *P. purpurogenum* series but closer identification is impossible.

Penicillium purpurogenum Fleroff-Stoll, was discussed in Biourge's Monograph (La Cellule **33**: fasc 1, pp. 235–237; Col. Pl. VII and Pl. XI, fig. 66. 1923) in terms which made impossible its separation from *P. purpurogenum* Stoll. Biourge's strain when studied in laboratory cultures confirmed this relationship.

Penicillium sulfureum Sopp (Monogr. pp. 172–173, Taf. XVII, fig. 120; Taf. XXIII, fig. 22. 1912) was included by Thom (1930) in his "*P. luteum* series—non-ascosporic." The production of red to blood red colors in the substratum as noted by Sopp, seems to align it with some member of the *P. purpurogenum* series. The isolate upon which the species was based probably represented some strain of *P. purpurogenum* or *P. rubrum* which was characterized by abundant yellow mycelium upon the particular substratum employed. More exact placement cannot be made.

Penicillium purpurogenum Stoll var. *rubri-sclerotium* Thom, in Mycologia **7:** 141–142, fig. 1. 1915; The Penicillia, p. 479. 1930.

Thom established this variety to include certain strains producing a cultural picture which he regarded as *Penicillium purpurogenum* Stoll, but which characteristically produced dark red to reddish brown sclerotia, at least when newly isolated. His culture, No. 2670, isolated in 1912 by Dr. Erwin F. Smith, was found by May, Herrick, and co-workers (1927, 1928, 1929) to produce gluconic acid and has been widely cited in biochemical literature in connection with this fermentation. This strain originally produced abundant sclerotia, but during the long period of subsequent laboratory cultivation it has completely lost its capacity to produce these, and it no longer develops the red colors which are typical of both the species and the variety. The culture, now maintained as NRRL 1064, produces light-sporulating, somewhat funiculose colonies in pale blue-green shades. Superficially there is little to suggest the original isolate, but penicilli are typically biverticillate and symmetrical and show sterigmata and conidia as in the original culture.

NRRL 1066, received in 1941 from Dr. R. M. Whelden, Harvard University, is regarded as representative of the variety, since it still produces limited numbers of dark red sclerotia. Even in this strain, however, a reduction in the number of sclerotia produced has become clearly evident over the last few years. Both of these cultures tend to develop funiculose colonies and show elliptical to subglobose conidia with walls smooth or nearly so. Examined today, and without reference to original cultural appearances, both strains would be regarded as representing members of the *P. funiculosum* series. NRRL 1132, cited as a variant strain of *P. funiculosum* (see p. 619) produces dark sclerotia in old cultures strikingly similar to those seen in NRRL 1066.

Penicillium rubrum Stoll, in Beitrage zur morphologischen und biologischen Charackteristik Penicilliumarten, Wurzburg, p. 35, Taf. I, fig. 7, Taf. III, fig. 3, Taf. IV, fig. 4. 1904. See Thom, U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, p. 39, fig. 7. 1910; and The Penicillia, p. 476. 1930.

Colonies on Czapek's solution agar growing restrictedly, attaining a diameter of 1 to 2 cm. in 12 to 14 days at room temperature, consisting of a basal felt up to 1 mm. deep and conspicuously furrowed in some strains, in others much thinner and almost plane, usually more or less zonate, developing abundant conidial structures throughout the colony or in localized areas, usually heaviest near the colony margin, conidial areas in yellow to gray-green shades near pea green to sage green (Ridgway, Pl. XLVII) with non-sporulating or lightly sporulating areas usually showing orange-red coloration from pigmented aerial hyphae; exudate usually limited in amount, in small droplets, reddish to bright red in color; odor indistinct; reverse bright orange-red to cherry red with surrounding agar colored in lighter tints of the same shades; conidiophores up to 200μ or more in length by 2.2 to 3.0μ, with walls smooth or occasionally appearing somewhat granular, arising from the substratum or from creeping or aerial hyphae sometimes more or less funiculose; penicilli biverticillate and symmetrical, usually consisting of a terminal verticil of 5 to 10 metulae, measuring about 8 to 10μ or even 12μ by 2.0 to 2.5μ; sterigmata lanceolate with apices tapered in the manner characteristic of the group, in verticils of 5 to 8, mostly 10 to 12μ by 2.0 to 2.2μ, in individual strains longer or shorter; conidia smooth-walled, variable in dimensions, from strongly elliptical 3.0 to 3.5μ by 2.0 to 2.5μ in some strains, to ovate or subglobose 2.2 to 2.8μ by 2.0 to 2.5μ in others.

Colonies on steep agar growing somewhat faster, up to 3.0 cm. in 2 weeks, similar to the above in pattern and texture, but often colored in lighter and duller shades and sometimes appearing tufted or funiculose in central

colony areas; reverse usually in duller shades of red than on Czapek; penicilli as described above.

Colonies on malt extract agar growing more rapidly, up to 6.0 to 6.5 cm. in two weeks, usually thinner, plane, with surface velvety, tufted or funiculose, conidial structures arising almost entirely from the substratum, less abundantly produced in the marginal colony areas; reverse showing red pigmentation in varying amounts, usually most pronounced in central areas; odor slightly fragrant, somewhat suggestive of apples; penicilli as described above.

Species description centered upon NRRL 1062, isolated in 1930 from "mildew" on currency paper from The Bureau of Printing and Engraving, Washington; and upon NRRL 2120 received in May 1945, from Dr. W. Lawrence White, Philadelphia Quartermaster Depot, as an isolate from cotton duck exposed in Panama. The species is approximated by two strains received in February 1946, from the Centraalbureau as *Penicillium crateriforme* Gilman and Abbott. These latter strains differ from the above primarily in producing mycelial felts of closer texture on Czapek and steep agars, and in producing longer sterigmata up to 12 to 15μ in length. There is no suggestion on any substrate of crateriform colonies, the character upon which the species name was originally based.

Penicillium rubrum Stoll, as the species is understood by us, is closely allied to *P. purpurogenum* of the same author and is distinguished from the latter species primarily by its smooth-walled conidia; grayish yellow-green rather than dark olive-green conidial areas; and the production of more or less red pigmentation in colony reverse on malt agar. Individual strains are encountered which completely bridge between the two species, and it is possible that they should be regarded as representing different aspects of the same species.

Like *Penicillium purpurogenum*, *P. rubrum* appears to be widely distributed in nature and may be isolated from soil or from various organic materials. It has been repeatedly isolated from moist paper stocks and from exposed fabrics subjected to weathering. Under such conditions, its presence is usually revealed by the development of conspicuous areas of red or reddish discoloration in the substrate.

Individual strains as isolated show considerable variation in rate of growth, colony texture, pigmentation, and to a lesser degree in microscopic details, yet obviously constitute members of a single species aggregate. NRRL 2123, isolated from cotton duck exposed in Florida, and submitted for identification by Professor Wm. H. Weston, is apparently characterized by an invertase deficiency. The strain develops in a manner characteristic of the species on media containing dextrose, but grows very sparsely and sporulates lightly upon all media containing sucrose as a source of carbon,

NRRL 1180, received from Dr. G. A. Ledingham in 1937, is representative of occasional strains which differ from the species in being less deeply pigmented in reverse. They differ further in producing colonies on Czapek with a strong admixture of yellow pigmented hyphae. Details of the penicillus and measurements of cellular elements are typical of the species. Cultures of this type, in which a yellow-green colony is associated with a red reverse have, in the past, been commonly assigned to Thom's (1930) "*Penicillium luteum* series—non-ascosporic." They may be regarded as transitional between *P. rubrum* Stoll and *P. variabile* Sopp, as the latter species is understood and presented in this Manual.

Penicillium aculeatum Raper and Fennell, in Mycologia, **40**: 535–538, fig. 10. 1948.

Colonies on Czapek's solution agar growing restrictedly (fig. 163A), about 2 cm. in 12 to 14 days at room temperature, consisting of a tough basal felt 1 to 2 mm. deep, variously buckled and wrinkled, irregular in outline, medium sporing and velvety in appearance in central colony areas, developing yellow-green shades near celandine to artemisia green (Ridgway, Pl. XLVII), often with a pinkish cast from a limited overgrowth of red-pigmented hyphae and embedded droplets of exudate; growing margins 2 to 3 mm. wide, white to slightly pink, often appearing somewhat tufted or funiculose; exudate abundant, almost uncolored to definitely vinaceous, occurring in small droplets and often becoming overgrown by conidial areas as these develop; odor almost lacking; reverse in vinaceous or purplish red shades approximating mineral red to dark mineral red (R., Pl. XXVII) in older areas, usually not strongly discoloring the surrounding agar; conidiophores arising primarily from the mycelial felt, short, commonly about 50μ, rarely up to 100μ by 3.5 to 4.0μ, with walls appearing somewhat granular; penicilli typically biverticillate and symmetrical (fig. 163C) but with fractional or monoverticillate structures commonly produced; metulae 8 to 12μ by 4.5 to 5.5μ, usually appearing definitely inflated; sterigmata 7 to 9μ by 3.0 to 3.5μ, often appearing somewhat swollen; conidia globose to subglobose, 3.0 to 3.5μ in diameter, with walls comparatively heavy and conspicuously echinulate (fig. 163C), borne in loosely parallel or tangled chains 75 to 100μ in length.

Colonies on steep agar growing somewhat restrictedly but more rapidly than on Czapek, radially furrowed with center somewhat raised, medium sporing throughout, in dull yellow-green colors as above but with reduced development of pink aerial hyphae and an almost complete absence of pink exudate, growing margin about 1 mm. wide, white; reverse usually in lighter shades than on Czapek; conidial structures generally intermediate in pattern between those developed on Czapek and on malt agar.

FIG. 163. *A* and *B*, *Penicillium aculeatum* Raper and Fennell, NRRL 2130; ten-day-old colonies on Czapek and malt agars. *C*, Detail of penicilli from a second typical strain, NRRL 2129, showing rough conidiophores, globose and conspicuously rough conidia, × 1000. *D* and *E*, *P. variabile* Sopp, NRRL 1048, ten-day-old colonies on Czapek and malt agars.

Colonies on malt agar spreading broadly, up to 5.5 to 6.0 cm. in 12 to 14 days, plane (fig. 163B), heavily sporing throughout, in dark yellow-green shades near Lincoln green to dusky olive green (R., Pl. XLI); conidiophores arising primarily from the substratum, less commonly from trailing or ascending hyphae, mostly about 200μ long, but ranging from 100 to 300μ or more by about 2.5 to 3.0μ in diameter, with walls commonly roughened; penicilli comparatively short, consisting of a terminal verticil of metulae bearing clusters of somewhat divergent sterigmata, but typical of the Biverticillata-Symmetrica; metulae occurring in verticils of 5 to 9, each bearing a crowded cluster of 5 to 7 sterigmata with finely granular walls and with strongly tapered conidium-bearing tips; conidia globose to subglobose, 3.0 to 3.5μ in diameter, conspicuously echinulate, dark olive green in mass, occurring in loosely parallel or tangled chains 100 to 150μ in length.

Species description based upon a number of strains received from Professor William H. Weston, Harvard University, as unidentified cultures isolated from canvas and other materials infected during exposure tests in Florida. NRRL 2129 and NRRL 2130 are representative. The species is regarded as new since careful examination of the literature has failed to reveal any described form which produces globose and conspicuously rough conidia and strongly roughened conidiophores in colonies with deep red colors in reverse.

The species name is taken from the Latin *aculeatus* (meaning "prickly"), and is applied because of the conspicuously echinulate character of conidia, and the roughened walls seen in conidiophores, metulae, and even sterigmata on malt agar where the species makes its maximum development.

Penicillium aculeatum is tentatively assigned to the *P. purpurogenum* series. Such placement is based upon two primary considerations: (1) colonies are more or less restricted on Czapek and steep agars and in reverse produce a rich red to purple-red coloration, and (2) colonies on malt agar are broadly spreading, heavily sporing throughout, dark yellow-green in color, and essentially velvety. It differs from the other members of this series in producing conidial structures with walls often roughened and with conidia strongly echinulate and *globose* rather than elliptical to subglobose. Elements of the penicillus are usually shorter and tend to be divergent rather than closely parallel. In this latter characteristic the species resembles *P. verruculosum* Peyronel (see p. 621), which likewise produces rough globose conidia. The comparatively short, broad penicilli are suggestive of the *P. herquei* series, but the species shows little additional evidence of relationship in that direction. *Penicillium aculeatum* is separated from the *P. funiculosum* series by an absence or limitation of funiculose hyphae. It is separated from the *P. rugulosum* series by the production of abundant red to purple-red color in colony reverse, and by the character

of its conidia. Despite the fact that the species does not conform very closely with other members of the *P. purpurogenum* series, it is our belief that mycologists and microbiologists encountering this species in culture will locate it here more conveniently than elsewhere.

Penicillium variabile Sopp, in Monogr., pp. 169–171; Taf. XVIII, fig. 124; Taf. XXIII, fig. 27. 1912. Thom, The Penicillia, pp. 477–478. 1930.

Colonies on Czapek's solution agar attaining a diameter of 2.5 to 3.0 cm. in 12 to 14 days, usually radially furrowed (fig. 163D), consisting of a fairly tough mycelial felt 200μ or more deep, appearing velvety or slightly granular, usually developing abundant conidial structures which may be concentrated in central colony areas, arranged in conspicuous zones, or irregularly produced in localized areas or patches, growing margin usually conspicuous, in white through cream to bright yellow shades, commonly 1 to 2 mm. wide; colonies variously colored, with heavily sporing areas ranging from sage green to slate olive or andover green (Ridgway, Pl. XLVII) and with lighter sporing areas near Hathi gray to storm gray (R., Pl. LII), commonly showing extensive non-sporulating areas (fig. 163D) variously colored in bright yellow, cream yellow, to orange buff shades depending upon the age and abundance of yellow encrusted sterile hyphae, sporulating and non-sporulating areas often intermixed to present a mottled appearance; exudate lacking or limited in amount, usually clear; odor not pronounced; reverse in yellow to orange-brown shades, often showing a greenish cast, less commonly orange-red; conidiophores arising from the mycelial felt, or in marginal areas of older colonies directly from the substratum, often short but sometimes up to 200μ or more in length by 2.5 to 3.0μ, smooth-walled, sometimes branched; penicilli typically biverticillately symmetrical, usually consisting of a single verticil of 5 to 7 metulae, varying in length from 7.5 to 10μ in some strains to 12 to 14μ in others; sterigmata typically lanceolate, tapered, in clusters of 5 to 7, measuring 10 to 12μ by 1.8 to 2.2μ conidia strongly elliptical, with ends often more or less pointed, mostly 3.0 to 3.5 by 2.0 to 2.5μ, but showing great variability in size, occasionally up to 7 to 8μ in long axis, with walls smooth or appearing irregularly roughened in very large conidia.

Colonies on steep agar 3 to 3.5 cm. in 2 weeks, plane or lightly furrowed, heavily sporing throughout, in dull yellow-green to gray-green shades, showing little or no admixture of sterile yellow hyphae in some strains, abundant in others; exudate lacking; odor indistinct; reverse in yellow-orange to dull brown shades, commonly more or less mottled; conidial structures as described above.

Colonies on malt agar (fig. 163E) essentially as on steep but with mar-

ginal areas usually somewhat thinner, plane, heavily sporing throughout, with yellow encrusted mycelium usually evident in marginal and submarginal areas; reverse in dull orange or orange-brown shades; penicilli as described above.

Species description based upon numerous strains examined during the present study, including: NRRL 1048, received in 1938 from J. W. Bowen, Johannesburg, South Africa, as an isolate from coconut matting; NRRL 1055, received in 1936 from E. F. Sprague, Los Angeles, California; NRRL 2124, received in May 1945 from W. Lawrence White, Philadelphia Quartermaster Depot as an isolate from an army cot in Florida.

Occasional strains are encountered, of which NRRL 1178 is representative, which differ from the species in producing colonies with little or no yellow encrusted mycelium, and with reverse usually uncolored or slightly greenish. However, central areas of old colonies show abundant yellow encrusted mycelia and rich orange-brown colors in reverse. Conidial structures duplicate those of the species in all essential characteristics. These strains must be regarded as representing a normal type of variation within the species.

Penicillium variabile, as presented here, includes most of the forms contained in Thom's "*P. luteum* series, non-ascosporic" (1930). As indicated elsewhere, however, this was a very general usage and included strains now assignable to *P. rubrum*, *P. verruculosum*, and possibly other species which sometimes produce colonies showing an abundance of yellow aerial mycelium. Furthermore, application of the name *P. luteum* for non-ascosporic forms is untenable, unless the origin of such strains can be verified, since this binomial was originally applied to a distinctive ascosporic form (see p. 602).

We clearly recognize that no sharp line of separation exists between the ascosporic and non-ascosporic series of the Biverticillata-Symmetrica, for undoubtedly strains once ascosporic are commonly isolated as the conidial stage only. Loss of ascospore production often occurs in cultures maintained in the laboratory, and it is reasonable to suppose that the same occurs in nature, although probably less commonly. In a single case the reverse is known to have taken place. NRRL 2125, originally isolated from canvas in Panama, was received in December 1945 from Professor Weston as a non-ascosporic culture typical of the strains assigned by us to *Penicillium variabile* Sopp. In a subsequent recultivation a few scattered yellow perithecia developed in colony centers on malt agar after three to four weeks. The possibility of contamination was eliminated by careful recultivation. Ascospores were elliptical and conspicuously roughened. The pattern of perithecial initials could not be determined since these developed only in heavily sporulating (conidial) areas. The compact and

somewhat restricted colonies of the strain are presumed to indicate closer relationship to *P. wortmannii* than to *P. vermiculatum*, but the conidial structures and the ascospores produced would satisfy either of these species. It is entirely possible that most of the cultures now assigned to *P. variabile* Sopp actually represent imperfect forms of one or more ascosporic species.

Penicillium citricolum Bainier and Sartory (Bul. Soc. Mycol. France **28:** 276–279, Pl. XIII, figs. 1 and 2. 1912) is believed to have been based upon a culture of the type included in *P. variabile* of this Manual. Colonies were described as blue-green on some media with reverse and medium citrine yellow; conidiophores were about 2μ in diameter, septate, more or less sinuous and rather long. Penicilli were figured as biverticillate and symmetrical, with 4–6 metulae in a single verticil; conidia were shown as strongly elliptical. Cultures have not been seen and exact identification is impossible.

Penicillium aureolimbum Zaleski (Bul. Acad. Polonaise, Sci.: Math. et Nat. Ser. B., pp. 481–482, Taf. 53. 1927) was assigned to the "*P. luteum* series, non-ascosporic" by Thom (1930) from Zaleski's description, but no satisfactory type was received and the description was not sufficiently explicit to guarantee the correctness of such placement. A culture subsequently received from Zaleski under this name proved to be *P. notatum* Westling. The nature of the species must remain in doubt.

Penicillium brasiliense Thom (The Penicillia, pp. 483–484, fig. 83. 1930) was based upon his No. 4707.759 I from Dr. daFonseca of Rio de Janeiro, Brazil. The species was described as follows: "Colonies white to very faintly tinged, velvety, spreading broadly, not over 200μ deep, slowly and incompletely zonate in age; reverse (four weeks) yellow to olive buff or a dirty yellow-orange mixture; drops not seen; odor none; conidiophores ascending rather than erect, 100 to 200μ long, by 3μ to 4μ, with walls pitted or rough; penicilli variously branched, only partly biverticillate; metulae 16 to 20μ, enlarged at the apex, unequal in the verticil; sterigmata 13 to 16μ in length; conidia about 3μ in diameter." The species was based upon a single culture, now lost from our Collection and not listed as available from Baarn. It was recognized to account for "white forms with partly biverticillate penicilli." Thom assigned the species to a miscellaneous biverticillate series, at the end of the Biverticillata-Symmetrica, which is not recognized in the present Manual. In view of the fact that Thom reported penicilli as only partly biverticillate, and in the absence of an authentic culture, proper disposition of *P. brasilicnse* must remain in doubt.

Occurrence and Significance

Penicillium purpurogenum and allied species represent normal components of the mycoflora of most soils, and may be expected to occur on almost any organic material that is subject to soil, air, or water-borne contamination. They are commonly observed in soil dilution plates where, upon most media, they appear as heavily sporing, deep yellow-green colonies with reverse usually in bright to deep red or reddish purple shades. Frequently they occur upon moist paper stocks, starch paste and other materials of like nature, appearing as deep greenish areas surrounded by halos of reddish color. Members of the series were common among the molds

isolated from deteriorating military equipment in tropical and subtropical areas and submitted for identification.

Strains of *Penicillium purpurogenum* not infrequently develop as parasites on species of *Aspergillus*, particularly members of the *Aspergillus niger* series (Thom, 1930). They seldom kill the host, but markedly restrict its growth and development. When present on strains used for acid production in industry, they seriously interfere with these fermentations. The characteristic picture of one of these molds parasitizing an *Aspergillus* is beautifully shown in a photograph by Dr. Edward Yuill reproduced in this Manual as figure 23.

Palei and Osuicheva (1936) isolated a heat-resisting substance (named "penicillin") from the metabolism solution of *Penicillium luteum-purpurogenum* which interfered with citric acid formation by *Aspergillus niger*.

Members of the present series, referred to as the *Penicillium luteum-purpurogenum* group, received considerable attention as producers of gluconic acid by May, Herrick, and others in the U. S. Department of Agriculture several years ago. One culture, *P. purpurogenum* var. *rubri-sclerotium*, Thom's No. 2670, gave unusually good yields of acid in surface cultures upon a solution containing 20–25 percent glucose and various inorganic salts (May, *et al.*, 1927). A year later Herrick and May (1928) defined the optimum cultural conditions for acid production by this strain, and in 1929 May, *et al.*, described production methods on a semi-plant scale using large shallow pans of high purity aluminum. When in subsequent work, selected strains of *P. chrysogenum* (May, *et al.*, 1934 and Moyer, *et al.*, 1936) and *Aspergillus niger* (Wells, *et al.*, 1937, Moyer, *et al.*, 1937, and Gastrock, *et al.*, 1938) were successively found to produce even higher yields in submerged culture, attention was naturally directed to them. The latter species is now generally used for the commercial production of gluconic acid.

Following the paper of May, *et al.* (1929), other workers erroneously adopted the designation *Penicillium luteum-purpurogenum* as a specific name to be applied to particular strains, presumed to belong to the species *P. purpurogenum* or the *P. purpurogenum* series. Angeletti and co-workers published a series of papers (1931, 1932a, 1932b, and 1934a) in which the production of various organic acids by a culture designated *P. luteum-purpurogenum* was reported. The addition of 0.01145 gm./l. of Fe (as $FeCl_3 \cdot 6H_2O$) was found to increase the yield of gluconic acid from glucose by 11.5 percent (1934b).

Yuill (1934) investigated acid production by a *Penicillium* "with affinities in the *P. luteum-purpurogenum* group" which was isolated as a parasite on *Aspergillus niger*. When the mold was grown in the presence of $CaCO_3$, the Ca salt of an acid insoluble in water but soluble in alcohol was formed

in addition to Ca citrate and traces of Ca oxalate. In the absence of $CaCO_3$ neither citric nor oxalic acid was detected, but the insoluble acid was deposited on the mycelium and fruiting structures. The substance, when purified, melted at 201–202°C., titrated as a tetrabasic acid on boiling, and upon micro-analysis gave the empirical formula $C_{18}H_{20}O_7$. It was regarded as probably identical with "glauconic acid I", earlier isolated by Wijkman (1931) from a culture reported as *P. glaucum*.

Waksman and Horning (1943) attributed some antibiotic action to *Penicillium luteum-purpurogenum*, but did not isolate the active substance.

Durrell (1930) reported *Penicillium purpurogenum* as a common parasite on maize seedlings, which in some cases reduced the stand by as much as 50 percent. As a control measure, mercuric dusts gave promising results.

Penicillium purpurogenum was found by de Lima (1943) to be one of three common molds capable of saccharifying the starch of cassava pulp preparatory to the production of the alcoholic beverage Tiquira. This species gave a conversion of 68.1 percent against 90 percent for *Monilia sitophila* and 64.7 percent for *Aspergillus niger*.

Brenner (1918) investigated the pigment produced by *Penicillium purpurogenum*, whereas Posternak (1939) studied pigment production in cultures identified as *P. rubrum* and *P. citreo-roseum*.

Hansel (1940) and Pennington (1941) reported airborne molds identified as *Penicillium rubrum* to be incitants of allergies in patients subject to hay fever or asthmatic symptoms. McMurray (1940) reported *P. rubrum* to be common in cases of otitis and recommended the use of a 45 percent alcoholic solution of phenylmercuric nitrate as a reliable therapeutic treatment.

Penicillium rugulosum Series

Outstanding Characters

Colonies on Czapek's agar growing restrictedly, variable in texture, ranging from closely woven and conspicuously wrinkled felts of sterile pigmented or encrusted hyphae to thin networks in which the vegetative mycelium is uncolored and largely submerged; sporulating irregularly, heaviest in colony centers, or sometimes in marginal to subcentral areas, conidial areas typically in dark or dull yellow-green shades; reverse variously colored in yellow to orange-brown or greenish shades, seldom showing true reds; often appearing more or less mottled.

Conidiophores commonly arising from the basal felt or from submerged hyphae, occasionally branched, with walls smooth or nearly so.

Penicilli typically biverticillate and symmetrical, usually consisting of a terminal verticil of metulae, but commonly developing fractional or irregular structures in some species and strains.

Conidia persistently elliptical, variable in size, with walls usually roughened but appearing smooth in some species and strains.
Odor usually lacking or indistinctive.

Series Key

1′. Colonies restricted, close-textured, usually strongly folded or wrinkled.
aa. Conidia elliptical, conspicuously rugulose; penicilli typically biverticillate-symmetrical but often irregular in pattern ..... *P. rugulosum* Thom
bb. Conidia strongly elliptical, smooth or slightly and irregularly roughened; penicilli more consistently biverticillate-symmetrical ... *P. variabile* Sopp (in the *P. purpurogenum* series)
2′. Colonies very restricted, or very thin and plane, but with central area commonly raised or floccose.
aa. Colonies very thin throughout or with central area somewhat floccose, growing more or less restrictedly upon all substrata ..... *P. tardum* Thom
bb. Colonies growing very restrictedly upon Czapek, but heavily sporing and broadly spreading on media containing ammonium nitrogen. *P. diversum* Raper and Fennell
1″. Colonies producing abundant yellow, much-branched mycelia on malt, often tending to characterize the culture. *P. diversum* var. *aureum* Raper and Fennell

The series includes a number of slowly growing forms which are regularly encountered in the mycoflora of soils. They appear to be widely distributed and occur with considerable frequency upon decaying vegetation and a variety of other organic materials subject to processes of weathering and slow decomposition. They have been repeatedly encountered among the Penicillia isolated from tentage and other protective fabrics in the field. Two fairly-well defined subseries are recognized:

The first of these is typified by *Penicillium rugulosum* Thom and is characterized by restricted, compact colonies on Czapek's agar which usually show an admixture of sterile, encrusted vegetative hyphae and dark yellow-green conidial heads in greater or less abundance. Colonies on malt agar are heavier sporing and usually somewhat faster growing, but remain restricted in comparison with species such as *P. funiculosum* and *P. purpurogenum* considered above. *Penicillium rugulosum* is characterized particularly by its strongly elliptical and conspicuously rugulose conidia.

The second subseries is typified by *Penicillium tardum* Thom and is characterized by very thin or extremely restricted colonies on Czapek's solution agar. In the species *P. tardum*, growth on all substrata is regularly restricted. In some other forms, colonies on nutrient-rich media such as malt agar are luxuriant, broadly spreading, and heavily sporing. Limited growth on Czapek's agar can be attributed to definite nutritional deficiencies in some cases, and when these are supplied, the thin or restricted forms may duplicate well-recognized species and thus be properly assigned. In

other cases the deficiencies may be identified, but the organisms still retain distinctive characteristics even after the deficiency has been removed. The description of a new species is then necessary. Such was the case with *P. diversum* Raper and Fennell. Extremely limited growth on Czapek and steep agars could be attributed to an inability to utilize nitrate nitrogen, since strains of this species grew normally when ammonium rather than nitrate compounds were supplied as a nitrogen source. A variety of *P. diversum*, *P. diversum* var. *aureum* was recognized by these authors to include occasional strains which exhibited the same basic characteristics but on some substrata showed a luxuriant development of sterile yellow aerial mycelium which effectively distinguished them.

Penicillium rugulosum Thom, in U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, pp. 60–61, fig. 21. 1910; The Penicillia, pp. 472–474, figs. 80 and 81. 1930.

Colonies on Czapek's solution agar growing restrictedly, attaining a diameter of 1.0 to 1.5 cm. in 12 to 14 days (fig. 164A), margins abrupt, colonies consisting of a fairly tough, closely woven, strongly wrinkled felt in white to flesh shades, in some strains bearing limited conidial structures to produce a light gray effect, in others producing abundant conidial structures in yellowish green to dark green shades approximating Russian green (Ridgway, Pl. XLII); exudate lacking or limited in amount; odor indistinct; reverse at first colorless or nearly so in most strains, becoming vinaceous or orange-red either in localized areas or throughout; conidiophores arising from the basal felt, sometimes branched, mostly less than 50μ in length but ranging up to 100μ by 2.5 to 3.0μ in diameter, walls smooth; penicilli typically biverticillate and symmetrical (fig. 164D), but sometimes fractional or irregular; metulae usually in verticils of 5 to 7, mostly 9 to 12μ by 2.0 to 2.5μ; sterigmata commonly in verticils of 5 to 8, acuminate, about 10 to 12μ by 1.8 to 2.2μ, but in individual strains often longer or shorter; conidia elliptical, 3.0 to 3.5μ by 2.5 to 3.0μ, with walls conspicuously roughened, in tangled chains up to 50μ or more in length.

Colonies on steep agar growing more rapidly, 2.5 to 3.0 cm. in diameter in two weeks, with limited central area raised, slightly floccose, dull gray in color and with marginal zone 1 cm. wide radially furrowed (fig. 164B), heavily sporing, in gray-green shades near artemisia to lily green (R., Pl. XLVII); colony reverse ranging from colorless or drab to more or less mottled in red and brown shades; penicilli as described above.

Colonies on malt extract agar growing at about the same rate as on steep agar but heavily sporing throughout (fig. 164C), plane, in dull yellow-green shades, appearing almost velvety but with surface regularly showing a thin loose network of white to yellow, sometimes encrusted aerial hyphae;

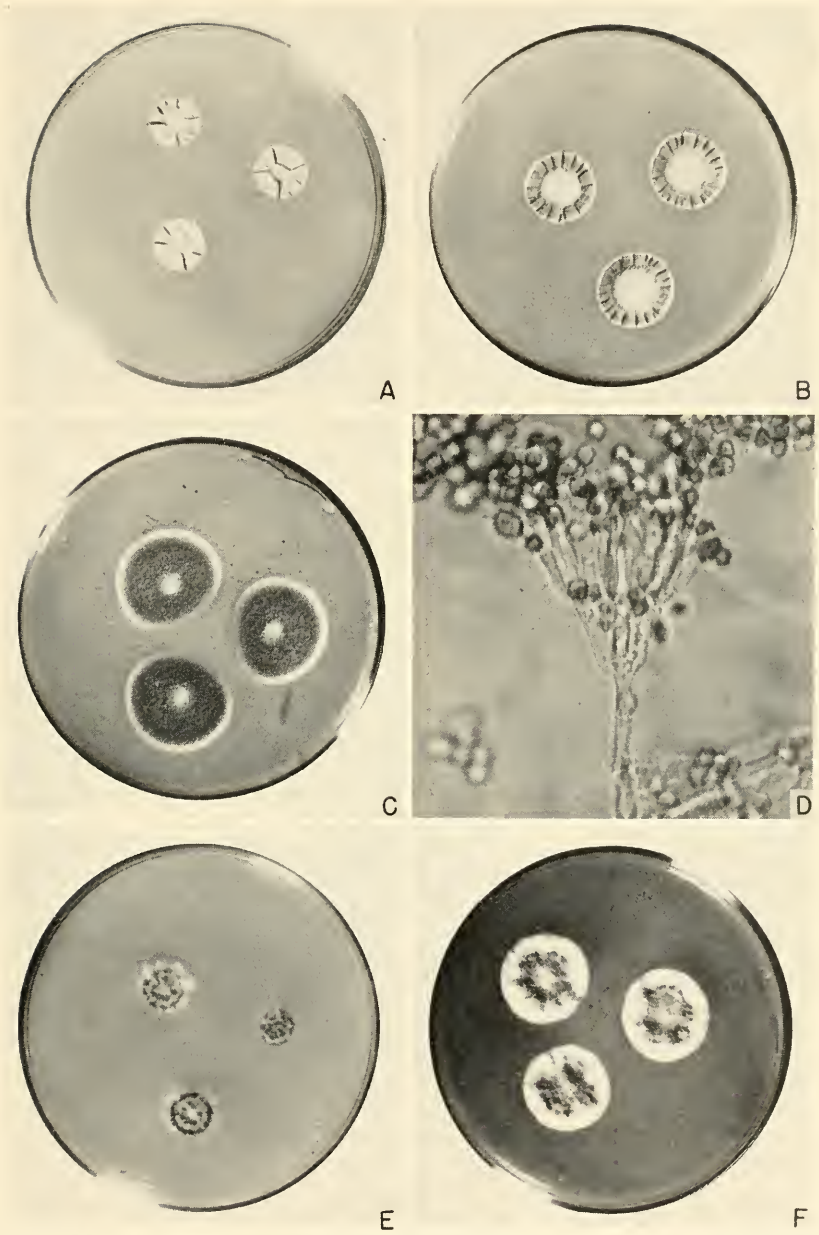


FIG. 164. *A*, *B*, and *C*, *Penicillium rugulosum* Thom, NRRL 1045, on Czapek, steep, and malt agars, respectively, at ten days. *D*, Detail of penicillus in same strain, × 900. *E* and *F*, *P. tardum* Thom, NRRL 1073, on Czapek and malt agars at ten days.

conidiophores longer than on Czapek, mostly 100μ long; penicilli as described above but showing conidial chains up to 150μ in length.

The species is distinguished particularly by its restricted growth and its strongly elliptical, rugulose spores. Species description centered upon the type culture, NRRL 1045 (Thom No. 46); NRRL 1047 from the Biourge Collection in 1924; and numerous others examined during this and earlier work. The species is approximated by NRRL 1157 received in 1936 from Dr. G. A. Ledingham, Ottawa, Canada, as an isolate from chickens in cold storage.

Penicillium rugulosum appears to be abundant in soil and in soil contaminated products and to be widely distributed. Cultures as newly isolated usually produce abundant conidial structures upon all common substrata, including Czapek's agar. When long maintained in culture, they often tend to sporulate less heavily and to develop deeper mycelial felts. The members of the species show a marked tendency to vary, and even in normal cultures the irregular coloration of the colony in reverse may indicate a degree of strain instability.

The following species, subsequently described by other investigators, are regarded as synonymous with *Penicillium rugulosum* Thom:

Penicillium crateriforme Gilman and Abbott (Iowa State College Jour. Sci. **1**: 293, fig. 28. 1927) was assigned to the *P. rugulosum* series by Thom (1930, p. 475). Reexamination of Gilman and Abbott's type, now maintained as NRRL 1057, confirms Thom's placement but fails to show sufficient differences to warrant species recognition. Colonies on Czapek are almost indistinguishable from those of NRRL 1045, the type of *P. rugulosum* Thom, and differ from the latter on steep and malt agars only in producing slightly faster-growing colonies and conidial areas in darker and less yellowed shades. Conidia are strongly elliptical and rugulose. The culture is regarded as representing a variation within the species *P. rugulosum* Thom.

Two strains received from the Centraalbureau under this name in February 1946, develop an intense red pigmentation on Czapek and steep agars, have smooth conidia and produce broadly spreading and heavily sporing colonies on malt with a pronounced apple to walnut odor. They are regarded as more nearly representing *Penicillium rubrum* Stoll in the *P. purpurogenum* series.

Penicillium chrysitis Biourge (Monogr., La Cellule **33**: fasc. 1, p. 252, Col. Pl. XI and Pl. XIX, fig. 112. 1923) from Biourge's description and his culture (now NRRL 1053), supplied to Thom in 1924, is closely related to *P. rugulosum* Thom, but shows slightly lighter colors in reverse. Recognition of this species would be warranted only if the strains which we have included under *P. rugulosum* were to receive names enough to cover all of the quantitative differences in color production.

Color Mutant: A tan-spored mutant, differing from the parent culture only in the coloration of conidia, has been isolated from the type strain of *Penicillium rugulosum* Thom, NRRL 1045.

Penicillium tardum Thom, in The Penicillia, pp. 485–487, fig. 84. 1930.
Synonym: *Penicillium elongatum* Bainier, in Bul. Soc. Mycol. France **23:** 17–18; Pl. V, figs. 1–7. 1907.

Colonies upon Czapek's solution agar growing very restrictedly, attaining a diameter of 1.5 to 2.0 cm. (fig. 164E) in 12 to 14 days at room temperature, usually with central areas raised, 1 to 2 mm. deep, floccose-funiculose, at first white but developing dull gray-green shades with the production of conidial structures, with marginal zone very thin, largely submerged, 2 to 4 mm. wide; in some strains with entire colony consisting of a very thin submerged mycelium producing scattered conidial structures usually more concentrated in central areas, irregularly gray-green to dark yellow-green in color from a limited production of conidial structures; odor limited or indistinct; exudate lacking; reverse uncolored to fairly bright yellow at colony centers, with green of conidial structures often showing through in marginal areas; penicilli typically biverticillate-symmetrical but often fractional, bearing conidia in long tangled or loosely parallel chains; conidiophores arising either from the substratum or from aerial hyphae, variable in length, commonly 100μ or less by 2.0 to 2.5μ in diameter, but occasionally up to 300 to 400μ long, smooth-walled; metulae in verticils of 5 or more in larger penicilli, mostly 9 to 12μ by 2.0 to 2.5μ; sterigmata closely parallel, in verticils of 5 to 7 or 8, lanceolate, typical of the group, mostly 8 to 10μ by 1.8 to 2.2μ, occasionally longer with long tapered conidium-bearing tubes; conidia elliptical, rarely subglobose, mostly 3.0 to 3.5μ by 2.0 to 2.5μ with walls comparatively heavy and somewhat roughened, dull olive-green in mass.

Colonies on steep agar as described above but quickly developing dull olive-gray shades with thin marginal zone often less conspicuous and tending to develop a limited floccose growth in age; reverse uncolored or showing drab to dull reddish shades; conidial structures as described above.

Colonies on malt agar growing more rapidly, about 3.0 to 3.5 cm. in two weeks, variable in pattern and texture depending upon the individual strain, in some tending to be floccose (fig. 164F) up to 2 mm. or more deep and sporulating irregularly to give the culture a zonate to mottled appearance, conidial areas in dull blue-green shades; in other strains colonies are less floccose, velvety or nearly so, heavier-sporing, in shades near sage green (R., Pl. XLVII), reverse in dirty cream to dull orange-brown shades; penicilli as described above.

Species description centered upon NRRL 1073, cited by Thom as one of the types (his No. 4640.444), and NRRL 2116 received from the Centraalbureau in July 1946, listed as having come from Thom in 1937 as

Penicillium tardum. These cultures may or may not have stemmed from the same original source. The species is approximated by NRRL 1052 (Thom's No. 4640.439), received in 1922 from the Bainier Collection as *P. atricolum*.

The above strains show definitely roughened conidia and, since one of these represents type material, it is assumed that the conidia in Thom's cultures were also rough, although this was not specifically stated. Several additional strains approximating the above have been examined in the current study. Others differ from them in producing conidia with heavy walls that are smooth or nearly so and colonies on malt agar in darker yellow-green shades. These latter forms are regarded as best considered with the species *Penicillium tardum*, and it is possible that the species description should be broadened to include forms with both rough and smooth conidia. NRRL 2117 is representative of the forms with almost smooth conidia.

Thom (1930) based his species *Penicillium tardum* upon a culture received from the Bainier Collection (Thom's No. 4640.444—NRRL 1073) as *P. elongatum* Bainier. Because of the prior use of that name by Dierckx for a different type of *Penicillium* (belonging to the *P. expansum* series, *q.v.*), Thom redescribed the species and, because of its slow development on Czapek's agar, applied to it the name *P. tardum*. Development of the species on other media was not discussed.

As newly isolated from nature, strains of *Penicillium tardum* typically produce very thin and somewhat restricted colonies on Czapek's agar with almost all vegetative mycelium submerged and conidial structures sparingly produced, and with these nearly always arising directly from the substratum. Strains long maintained in laboratory culture, such as NRRL 1073, commonly show a limited adaptation to synthetic media and gradually develop progressively larger and more flocculent colonies in which the marginal area only may retain the original appearance.

In the period since *Penicillium tardum* was described, it has been common practice in this Laboratory to assign to this species all strains that grow sparsely on Czapek's solution agar and produce typical biverticillate and symmetrical penicilli. As nutrient deficiencies have become better understood as factors affecting rates of growth and colony appearance in the Penicillia, some cultures previously assigned here have been found to represent deficient strains of other species of the Biverticillata-Symmetrica which are incapable of elaborating necessary amino acids, enzymes, or vitamins. Before assigning a strain to *P. tardum*, therefore, every possible effort should be made to identify whatever deficiency is responsible for its limited or restricted growth. If a deficiency is found, the strain, when grown upon non-deficient media, should be carefully compared with other

recognized species in the Section. If cultural and structural individuality still persists, as in the case of *P. diversum*, recognition of a new species would seem warranted.

Penicillium rugulosum var. *atricolum* (Bainier?) Thom. (The Penicillia, p. 474. 1930) was recognized by Thom in 1930, to cover a culture received from the Bainier Collection labelled *P. atricolum* which showed numerous characteristics relating it to his *P. rugulosum*, but developed colonies somewhat flocculent and colorless in reverse. Careful comparative examination of this culture, now NRRL 1052, fails to show any outstanding differences to separate it from typical strains of *P. tardum* Thom, hence continued recognition of the variety appears to be unwarranted.

Penicillium scorteum Takedo, Suematsu, and Nakazawa (Jour. Agr. Chem. Soc. Japan. **10**: 95–121. 1934) was isolated from military equipment and described as new. The type was received by Thom from Westerdijk in January 1937, and was noted at that time to approximate *P. pinophilum* Hedgcock. Re-examination of this strain upon different substrata for the current study shows it to be more closely allied to *P. tardum* Thom since it grows very restrictedly upon Czapek and steep agars but luxuriantly upon malt. Our culture, NRRL 1129, differs from most Penicillia in commonly producing conidia from *Cadophora*-like sterigmata, *i.e.*, sterigmata within which conidia appear to be formed and to be pushed out as they approach maturity.

Penicillium diversum Raper and Fennell, in Mycologia, **40**: 539–541, fig. 11. 1948.

Colonies on Czapek's solution agar extremely slow-growing (fig. 165A), 2 to 5 mm. in 12 to 14 days at room temperature, consisting of a fairly tough mycelial felt, surface appearing velvety or slightly granular, heavily sporing in yellow-green shades near Andover green (Ridgway, Pl. XLVII); exudate lacking; odor suggesting sea-weed; reverse uncolored; conidiophores arising from the mycelial felt, up to 200μ by 2.0 to 2.5μ, with walls smooth or nearly so; penicilli typically biverticillate and symmetrical (fig. 165C), regularly consisting of a terminal verticil of 5 to 7 or 8 metulae measuring about 9 to 11μ by 2.0 to 2.5μ, slightly enlarged upward; sterigmata usually in compact clusters of 6 to 8, mostly 8 to 10μ by 1.8 to 2.2μ; conidia at first elliptical, becoming subglobose or broadly elliptical when mature, with walls thin, smooth or delicately roughened, mostly 2.0 to 2.5μ by 1.5 to 2.0μ, borne in tangled chains up to 75 or 100μ in length.

Colonies on steep agar essentially as on Czapek but usually lighter sporing, conidial structures sparsely produced, often smaller than on Czapek.

Colonies on malt extract agar spreading broadly, up to 5.0 to 5.5 cm. in 12 to 14 days, velvety, plane, with vegetative mycelium largely submerged, bearing abundant conidial structures in a dense stand (fig. 165B), consistently narrowly zonate, heavily sporing throughout in dull gray shades near grayish olive (R., Pl. XLVI); showing abundant short, encrusted and pigmented hyphae intermixed with conidial structures; exudate

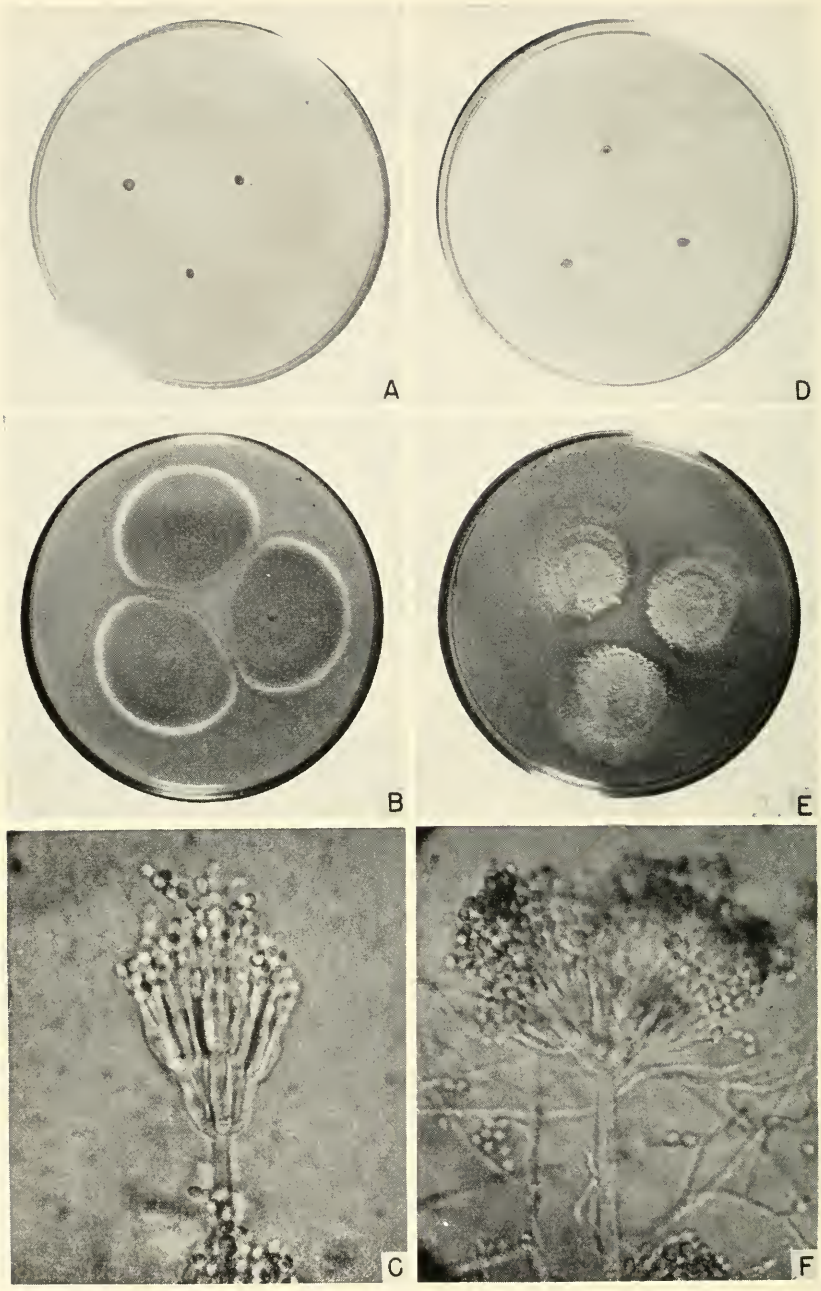


FIG. 165. *A* and *B*, *Penicillium diversum* Raper and Fennell, NRRL 2121, on Czapek and malt agars at ten days. *C*, Detail of penicillus of same strain, × 1000. *D* and *E*, *P. diversum* var. *aureum* Raper and Fennell, NRRL 1074, on Czapek and malt agars. *F*, Penicillus of the latter strain, which is very compact and characterized by a large number of metulae, × 1000.

lacking; odor not pronounced, slightly musty; reverse uncolored; conidiophores up to 300μ in length; penicilli as described on Czapek but generally showing metulae and sterigmata slightly longer; conidia in loosely parallel chains up to 200μ in length.

Colonies on Czapek's solution agar containing ammonium sulfate (3 g./liter) as the nitrogen source approximating those on malt in rate of growth, general texture, and in the abundance of conidial structures produced; conidial areas near Andover green (R., Pl. XLVII) showing a limited development of sterile, yellow pigmented aerial hyphae in submarginal areas; exudate lacking; odor indistinct; reverse uncolored; penicilli as described on malt agar.

Species description centered upon numerous strains isolated from various sources, including deteriorating military equipment, dried egg powder and soils. Also represented by several strains of unknown origin submitted for identification. The species is represented in our Collection by NRRL 2121, isolated from moldy leather and submitted to us for identification by Dr. T. C. Cordon, Eastern Regional Research Laboratory; NRRL 2122, isolated from soil collected in Sweden and contributed by Professor Edy Velander, Stockholm, and others.

This species is placed in the *Penicillium tardum* series primarily because of its very restricted growth upon standard Czapek's and steep agars containing nitrate as a nitrogen source. The fact that the species grows luxuriantly upon malt extract agar and upon Czapek's solution agar containing ammonium nitrogen clearly demonstrates the presence of a nutrient deficiency. Recognition of the species as new is based not upon its limited ability to utilize nitrate nitrogen, but upon its failure to duplicate any recognized form even upon media containing ammonium nitrogen where it grows luxuriantly. The species is clearly different from *P. tardum* Thom: penicilli are more consistent in pattern; conidia are smaller, less definitely elliptical, thin-walled, and smooth; and colonies upon favorable media are spreading, plane, heavy sporing, velvety, and zonate.

The binomial, *Penicillium diversum* (from the Latin *diversus*) is based upon the markedly different growth of this species upon different substrata.

Penicillium diversum var. *aureum* Raper and Fennell, in Mycologia, **40**: 541–542, fig. 11. 1948.

Colonies on Czapek's solution and steep agars duplicating those of the species in color, texture, and rate of growth (fig. 165D; cf. 165A); producing a fairly dense stand of conidial structures which differ from the species in showing metulae and sterigmata more numerous in the verticil and usually somewhat shorter.

Colonies on malt agar duplicating those of the species in rate of growth

but differing markedly in color and texture (fig. 165E), approximating olive yellow to olive ocher (Ridgway, Pl. XXX), appearing somewhat granular or tufted, especially in marginal areas, and consisting of a comparatively thin, closely interwoven network of yellow encrusted, much-branched, sterile hyphae enmeshing and largely obscuring numerous conidial structures; penicilli biverticillate and symmetrical, short and very compact (fig. 165F), bearing metulae in large crowded clusters of 12 to 15 or more, individually measuring about 7 to 8μ by 1.5 to 1.8μ; sterigmata in verticils of 6 to 8, about 7.5 to 9.0μ by 1.5μ, lanceolate with characteristically tapered tips; metulae and sterigmata usually yellowish green in color; conidia elliptical to subglobose, mostly 2.4 to 2.8μ by 2.0 to 2.5μ with walls comparatively thin, smooth or nearly so, in yellow-green shades.

The varietal name is based upon a characteristic yellow coloration upon certain media, including malt extract and Saboraud's agars. The variety differs from the species principally in the production of greatly increased amounts of yellow encrusted mycelium, and in the production of more compact penicilli consisting of substantially greater numbers of metulae and sterigmata.

Growth is more luxuriant when cultivated upon media containing ammonium instead of nitrate nitrogen, but unlike the species, growth upon this type of substrate does not equal that upon malt agar. The variety, however, obviously possesses the same basic nutritional deficiencies as the species.

The variety is represented by NRRL 1074, received in 1934 from R. W. Davidson, Division of Forest Pathology, Bureau of Plant Industry. The strain was initially diagnosed as *Penicillium tardum* Thom upon the basis of its symmetrically biverticillate penicilli and its restricted growth on Czapek's agar. The subsequent discovery and recognition of *P. diversum* Raper and Fennell, showed the true relationship of the variety to be with this species rather than with *P. tardum* Thom.

Occurrence and Significance

Members of the *Penicillium rugulosum* series appear to be abundant in all soils, and in addition commonly occur upon a wide variety of organic substrata including vegetable materials, stored grain, leather, tentage, and various other types of military equipment exposed to weathering processes. Like the *P. citrinum* series, these molds seem to be especially adapted to growth under conditions of limited nutrients and variable moisture. Their actual role in decomposition processes has received comparatively little attention.

McBeth and Scales (1913) and Scales (1915) reported *Penicillium rugulosum* as one of several species able to decompose cellulose. Thom (1930)

found the same species and other related forms on leather but reported little evidence of serious damage. Rennerfelt (1938), studying the interrelation between *P. rugulosum* and other micro-organisms, in laboratory culture, reported that the color of the *Penicillium* mycelium ranged from grayish green to brick red depending upon the carbohydrate supplied.

Penicillium rugulosum occasionally parasitizes other molds, particularly members of the *Aspergillus niger* group (Thom, 1930 and Romankova, 1936). In the commercial production of citric acid from sugar solutions, colonies of this species are reported to produce circular areas of infection in the floating blanket of *Aspergillus* mycelium which appear to rot and drop away when the mycelium is disturbed. Yields of acid are substantially reduced. In plate or tube cultures the *Aspergillus* colony may become penetrated by dense mats of *Penicillium* hyphae which envelop the stalks and fruits as densely radiating conidial structures, with the green penicilli of the parasite often masking the black heads of the *Aspergillus* (fig. 23). The development is not unlike that of *P. purpurogenum* Stoll under similar conditions.

Molds on military instruments represented the subject of an investigation by Takeda, Suematsu, and Nakazawa in 1934. Two new molds were described including a species of *Penicillium*, *P. scorteum*, that closely approximated *P. tardum* Thom. The use of wax containing 1 percent *p*-nitrophenol was recommended as a preservative for instruments. Growth of the mold was prevented by addition of 0.5 cc. chloropicrin or 20 gms. of *p*-dichlorobenzene per cubic meter of air.

Oxford and Raistrick (1934) investigated the biochemistry of *Penicillium crateriforme* Gilman and Abbott, a form which we now believe to have approximated *P. rugulosum* Thom (see p. 650). When grown upon a Czapek-Dox solution containing glucose as the sole source of C, spiculisporic acid ($C_{17}H_{28}O_6$), succinic acid, and a complex polysaccharide were produced. The first of these products was initially isolated from *P. spiculisporum*, hence the name (Clutterbuck, Raistrick, and Rintoul, 1931). Chopra and Ray (1939) studied the production of a red pigment by a *Penicillium* isolated in the Punjab and reported as *P. crateriforme* Gilman and Abbott. The pigment was readily produced when methyl, ethyl, or amyl alcohol, glycerol, or tartaric or citric acids were used as a source of C, although growth was most prolific when various carbohydrates were used. Amino acids, peptides, and peptone afforded more suitable sources of N than inorganic salts. Yields of 0.1 gm./l. of crude pigment were obtained. It melted at 180–200°C. and was oxidized to a colorless compound upon boiling with H_2O_2.

Johns, Philpot, and Pollock (1946) reported the production of "penicillin-like" antibiotics by different Penicillia including one from the Centraal-

bureau as *Penicillium crateriforme* G. and A. (Dattilo-Rubbo's strain). When examined by us, this same strain was diagnosed as approximating *P. rubrum* Stoll (see p. 637).

Penicillium herquei Series

Outstanding Characters

Colonies deeply velvety to almost lanose, less commonly floccose; with vegetative hyphae usually in shades of yellow-green to bright green; conidia in dull yellow-green shades; reverse dark yellow-green to brown or almost black.

Conidiophores arising from the substratum or the basal felt, comparatively long and coarse, usually roughened, at least in the terminal area.

Penicilli typically biverticillate and usually symmetrical or nearly so, but with metulae comparatively coarse and often more or less divergent.

Sterigmata in large clusters, not characteristically lanceolate but tapered abruptly to narrow conidium-bearing tubes.

Sclerotium-like masses of heavy-walled, polygonal cells produced in some strains and species; black to dark brown, usually elongate, and often partially buried in the substratum.

Series Key

3. Vegetative mycelium typically in yellow-green shades; conidiophores long and coarse, usually roughened; reverse dark but seldom developing true reds. *P. herquei* series
   a. Sclerotia lacking or rarely produced and limited in number; metulae numerous and somewhat divaricate; conidia elliptical.
      1′. Conidiophores usually less than 1 mm. in length and 4.0 to 4.5μ in diameter. *P. herquei* Bainier and Sartory
      2′. Conidiophores commonly 1 mm. or more and up to 2 mm. in length by about 8μ in diameter. *P. olsoni* Bainier and Sartory
   b. Sclerotia very abundant, characterizing the species; metulae 3 to 5 in number, in compact verticils; conidia globose. *P. novae-zeelandiae* van Beyma

Members of the series occur rather infrequently in almost all soils examined, and are occasionally isolated from decaying vegetation, fruits, exposed tentage and fabrics, wood, and other organic materials undergoing slow decomposition. They appear to be widely but not abundantly distributed in nature. Once encountered, they are easily recognized, for the bright yellow-green colors that characterize the vegetative mycelium, and usually the colony reverse, are not encountered elsewhere in the genus *Penicillium*. Conidial structures are also comparatively coarse and are not easily mistaken for those of other series either within or outside the Biverticillata-Symmetrica.

Three species are recognized, namely: *Penicillium herquei* Bainier and

Sartory, *P. olsoni* of the same authors, and *P. novae-zeelandiae* van Beyma. The first of these is known in culture from many strains and shows the general characters of the series itself. The second species, *P. olsoni*, is closely related to *P. herquei* and may, in fact, be based upon unusually coarse variants of the latter species. It is known from the original description and a culture which was for many years maintained in the Thom Collection. The third species, *P. novae-zeelandiae*, is known only as the type strain. It is of rather uncertain relationship, and assignment to the series with *P. herquei* represents a matter of expediency rather than a conviction of close kinship. The species is characterized particularly by the production of abundant black sclerotium-like masses of specialized thick-walled cells. Comparable structures are occasionally seen in limited numbers in both the *P. funiculosum* and the *P. purpurogenum* series, and from description are known to have occurred also in a culture diagnosed as *P. olsoni* Bainier and Sartory (see p. 664).

The *Penicillium herquei* series is included in the Biverticillata-Symmetrica upon the basis of the following characters: Penicilli are typically biverticillate and are usually symmetrical or nearly so, colonies typically produce varying amounts of yellow encrusted hyphae, particularly upon malt extract agar, and many strains produce a fragrant or aromatic odor suggesting apples or black walnuts. They differ from the more typical members of this Section, however, in producing relatively shorter and broader penicilli in which the number of metulae and sterigmata is commonly much greater than in other series or species, with the possible exception of *P. avellaneum* Thom and Turesson. In fact, there is a limited but definite degree of similarity between the penicilli of these forms. In both species, penicilli are comparatively large and compact and are borne upon long coarse conidiophores. Furthermore, metulae in both cases sometimes arise laterally as well as terminally from the apical portion of the conidiophore.

The relatively short, compact penicillus of *Penicillium herquei* is somewhat suggestive of the *P. brevi-compactum* series in the Asymmetrica-Velutina. However, such similarities as exist between these series are regarded as largely coincidental.

Penicillium herquei Bainier and Sartory, in Bul. Soc. Mycol. France **28:** 121–126; Pl. VII, figs. 1–10. 1912. See also Sartory and Bainier, Compt. Rend. Soc. Biol. Paris, **71:** 229–230; and Thom, The Penicillia, pp. 467–469, fig. 78. 1930.

Colonies on Czapek's solution agar (Col. Pl. X) growing slowly, attaining a diameter of 2 to 3 cm. in 2 weeks at room temperature (fig. 166A), often somewhat radially wrinkled, azonate or slightly zonate, deeply velvety to

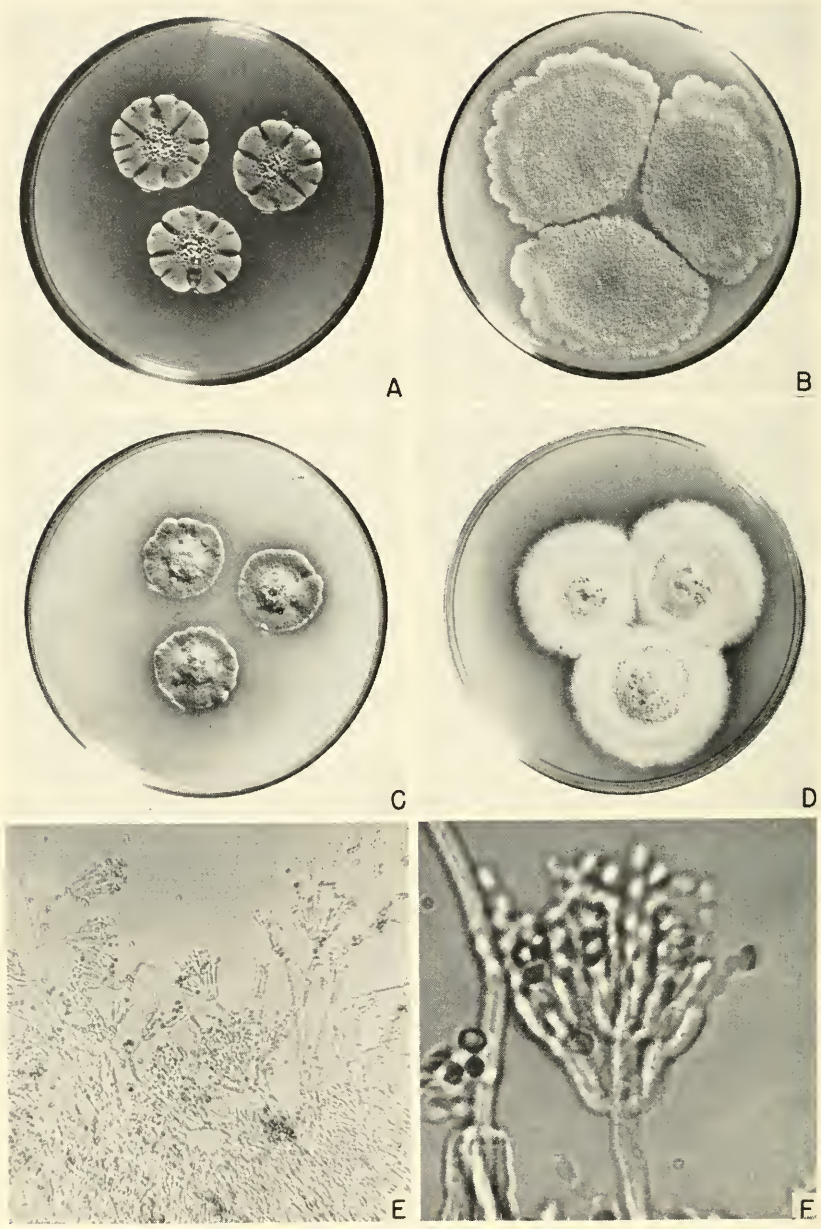


FIG. 166. *Penicillium herquei* Bainier and Sartory. *A* and *B*, Ten-day-old colonies of NRRL 1041 on Czapek and malt agars. *C* and *D*, Heavily sporing and floccose variants, respectively, of a second strain, NRRL 1138. *E*, Penicilli as seen under low power, liquid mount, × 200. *F*, Penicillus, × 750.

almost lanose, consisting of a thin basal felt with conidiophores arising from the felt or directly from the substratum, medium to heavy sporing, in yellow-green shades near tea green through vetiver to Andover green (Ridgway, Pl. XLVII); exudate lacking or limited; odor sometimes lacking or indefinite but usually strong, variable, often suggesting black walnuts, occasionally apples, or in some strains spicy; reverse in dark yellow-green (sometimes almost fluorescent) shades, becoming brown at margins, or occasionally under the entire colony, surrounding agar highly colored in lighter tints of the same shades; conidiophores 200 to 300μ or more in length by 3.5 to 4.5μ in diameter, appearing extremely rough and heavily encrusted when viewed dry under the low powers of a compound microscope, but in liquid mounts often appearing smooth, or again showing a coarse roughening immediately below the penicillus; penicilli comparatively short (fig. 166E and F), regularly consisting of a terminal verticil of metulae bearing clusters of sterigmata; metulae usually in verticils of 4 to 6 but sometimes up to 8 or 10, commonly measuring 10 to 15μ by 4.0 to 4.5μ somewhat enlarged at the tips; sterigmata 9 to 12μ by 3.0 to 4.0μ, in clusters of 8 to 12, tapered abruptly to narrow beak-like conidial tubes; conidia elliptical, typically smooth or nearly so, 3.5 to 4.0μ by 2.2 to 3.0μ, borne in tangled or loosely parallel chains up to 100μ or more in length.

Colonies on steep agar growing more rapidly, 3.5 to 5.0 cm. in 2 weeks at room temperature, deeper than on Czapek, with conidiophores up to 500 or 600μ long; exudate lacking or limited in amount; odor not as distinctive as on Czapek, with only an occasional strain suggesting black walnuts; reverse and details of penicilli as described above.

Colonies on malt extract agar spreading, 6 to 7 cm. in 2 weeks at room temperature, plane, very deeply velvety to lanose (fig. 166B), medium to heavily sporing with yellow encrusted mycelium fairly conspicuous throughout; odor not pronounced, usually somewhat unpleasant, occasionally with slight suggestion of walnuts; reverse in orange or greenish brown shades; conidiophores up to 1000μ or more in length; other details as described on Czapek's agar.

Species description centered upon NRRL 1040 from the Thom Collection as No. 4640.447, received originally from Bainier as his type; duplicated essentially by NRRL 1041, from the Thom Collection as No. 12719.7 isolated from wood by C. J. Humphrey at Madison, Wisconsin and cited in Thom's Monograph (pp. 469–470) as possibly representing *Penicillium lemoni* Sopp; NRRL 1837, from C. F. Andrus, Charleston, S. C., in 1942 as an isolate from marsh forest soil; and a strain received from the Centraalbureau as *P. hcrquei* and now maintained as NRRL 2113. This latter culture is listed as having been received from Paris in 1922 and may represent Bainier's type culture, thus duplicating NRRL 1040 in origin as well as in

cultural and microscopical characters. NRRL 1043 received from Professor Westerdijk in 1930 exactly duplicates these strains.

Cultures differing from the above, but obviously closely related, include:

NRRL 1765, received in 1941 from C. W. Hesseltine as an isolate from Wisconsin soil which differs from typical strains by producing more restricted colonies that are somewhat darker green in color, and produce conspicuously roughened conidia.

NRRL 2114, from Professor W. H. Weston as an isolate from deteriorating military equipment, differs from typical strains in producing very restricted, non-sporulating, colorless to yellow colonies on Czapek's agar and larger colonies of the same general texture, with marginal areas in blue-green shades near verdigris to zinc green (R., Pl. XIX) on steep agar; colonies on malt are typical of the species except somewhat lighter sporing and show an increased development of yellow mycelium.

NRRL 1042 from the Thom Collection as *P. lemoni* Sopp (Thom's No. 5320. Tal) differs in producing deeper, rather floccose colonies in zinc green shades (R., Pl. XIX) and with limited conidial structures borne on long conidiophores; the colony reverse is in deep greenish black shades.

The correct placement of *Penicillium herquei* Bainier and Sartory remains somewhat in doubt. Penicilli typically consist of terminal verticils of metulae bearing sterigmata and conidia in tangled chains, and are usually symmetrical in pattern. Furthermore, colonies normally show yellow encrusted hyphae more or less abundantly, especially in older colonies on malt extract agar. Many strains produce a definitely fragrant odor suggesting black walnuts or apples, as in the *P. purpurogenum* series. These characters seem to relate the species to the Biverticillata-Symmetrica where it was placed by Thom in 1930. The sterigmata of this species, however, are clearly different from those of typical members of that section, and the penicilli are usually more divaricate, as shown by Bainier's original figures. If assigned outside the Biverticillata-Symmetrica (considered but not proposed), the series would seem to fit best either as a separate series in the Asymmetrica-Velutina or possibly as a long-stalked member of the *P. brevi-compactum* series.

Penicillium herquei Bainier and Sartory is regarded as representative of a rather variable series of strains characterized by fairly short and compact penicilli, long roughened conidiophores, and colonies with a dark yellow-green coloration in reverse and commonly in the aerial vegetative mycelium of more floccose cultures as well. Individual strains vary appreciably in colony texture and in overall pattern, depending upon the relative abundance of fruiting structures and sterile pigmented hyphae. Thom, in 1930, included five species in his "*P. herquei* series," including *P. aureum* Corda, *P. lemoni* Sopp, *P. elegans* Sopp, and *P. olsoni* Bainier and Sartory,

in addition to *P. herquei*. All of these species were recognized as possessing essential characteristics in common with separation of *P. elegans* and *P. olsoni* based upon longer conidiophores up to 2 mm. Careful comparative study of cultures maintained in our Collection under some of the above names fails to show consistent differences: for example, NRRL 1040 and 1043, long maintained as *P. herquei* Bainier and Sartory and *P. elegans* Sopp respectively, now produce cultures that are identical in all measurable respects. Furthermore, individual strains which typically reproduce the cultural picture of *P. herquei*, as given by Thom in 1930, commonly develop sectors of variant growth types which can often be separated and perpetuated as separate and distinct strains. Thus, from culture NRRL 1138, diagnosed as typical *P. herquei* (fig. 166E), was obtained a much deeper floccose colony (fig. 166F) with very long conidiophores, and which produces a fragrant, ethereal odor which might approximate Sopp's "wonderful rose oil odor" attributed to his *P. lemoni*. It is believed significant that this variant duplicates almost exactly a strain, NRRL 1042, formerly maintained as *P. lemoni* Sopp.

A number of species showing a certain degree of individuality have been described which are now regarded as representing hardly more than normal variants within a broad interpretation of *P. herquei* Bainier and Sartory. The species listed below are believed to have been based upon such cultures. Strains have been encountered which in general satisfy the authors' description for the different species, yet fail to show characters adequate to distinguish them when considerable numbers of cultures are grown in parallel culture and compared.

Penicillium aureum Corda (Prachtflora, pp. 37–38, Taf. XVIII, figs. 1–3. 1839; Thom, The Penicillia, p. 469. 1930) is known only from the original description. It was reported in terms which lead us to believe that it represented some large, coarse member of this series characterized by golden yellow to bright yellow-green mycelium. Duplication of Bainier and Sartory's *P. herquei* is not claimed, but we regard it as probable that Corda's description was based upon a closely related form.

Penicillium elegans Sopp (Monogr., pp. 144–145, Taf. XVI, fig. 112; Taf. XXII, fig. 13. 1912; Thom, The Penicillia, p. 470. 1930) was described as deeply blue-gray to yellowish green, with culture reverse in yellow-green shades; vegetative hyphae were coarse and conidiophores were reported to be very long, uniform in diameter, septate, coarse, and somewhat roughened; sterigmata were very numerous, short, and produced elliptical conidia 3.5μ to 4.0μ in diameter. Occasional cultures are encountered which suggest Sopp's description but type material was never distributed and the species cannot be identified closer than to the *P. herquei* series.

Penicillium lemoni Sopp (Monogr., pp. 194–196; Taf. XX, fig. 152; Taf. XXIII, fig. 39. 1912; Thom, The Penicillia, pp. 469–470. 1930) was described as producing a network of dull green to yellow-green hyphae, with colonies yellowish to reddish brown in reverse, and conidiophores coarse, rough-walled and septate; penicilli were

manifestly biverticillate; perithecia (sclerotia) were observed and reported to consist of thick-walled parenchyma-like cells held together in clumps by reddish brown hyphae. The species was reported to produce a "wonderful rose oil odor," a characteristic which is rather common to several members of the Biverticillata-Symmetrica. The species is regarded as inseparable from *P. herquei* Bainier and Sartory.

Penicillium olsoni Bainier and Sartory, in Ann. Mycol. **10:** 398–399; Pl. VI, figs. 1–8. 1912; Thom, The Penicillia, pp. 471–472. 1930.

This species is regarded as closely related to *Penicillium herquei* Bainier and Sartory, but separable from it primarily upon the basis of its longer and very coarse conidiophores. No culture representative of the species has been available for the present study, and the following species diagnosis is based upon the original description, and Thom's notes on a culture which he believed to represent this species (Monograph, pp. 471–472. 1930).

Bainier and Sartory's description (condensed in Thom's Monograph):

"Colonies on banana forming tufts bluish (compare C.d.C. 378[1]) becoming grayish blue-green (C.d.C. 372, 373) in age sordid yellow-green; conidiophores erect, rigid, up to 8.4μ in diameter and comparatively very long, branches wanting or produced occasionally in age far down on the stalk and bearing a secondary penicillus; penicillus 2 to 3 times verticillate, usually symmetrically, occasionally with a superposed verticil on the main stalk prolonged; branches in the primary verticil (metulae?) up to 12 or more in number 8.4 to 11.2 by 3.2 to 5.6μ bearing either a secondary verticil of shorter and smaller metulae or sterigmata 4 to 6 in the verticil 8.4 to 11.2μ in length with long tapering points bearing the conidia; conidia ovoid, averaging 3.2 by 2.8μ; sclerotia and perithecia not reported."

Thom's notes on a culture (his No. 4725.1021, now lost from the Collection) from C. G. Hansford in Jamaica, which produced conidial structures with the characters of *P. olsoni*, follow:

"Colonies in Czapek's solution agar spreading broadly in its conidial stage, bluish green, loosely velvety, forming a mass of loosely standing stalks up to 2 mm. deep, with rather thin margin, later with the development of an overgrowth of ropes and tufts and masses of hyphae with sporadically at least the development of sclerotia or perithecia, black, more or less submerged, brittle but so far as studied producing no asci; reverse pale yellow to red or reddish in areas; conidiophores long, coarse, 500 to 1000 or even 2000μ by 8μ unbranched, colorless, smooth; penicillus biverticillate, or in some triverticillate, consisting of a crowded verticil of diverging metulae about 10 to 12μ in length, and much smaller in diameter than the stalk, bearing the sterigmata or occasionally with secondary verticils of shorter cells 8 to 10μ long, bearing the sterigmata; sterigmata up to 10μ long, more or less long pointed; conidia elliptical to almost globose 3 to 3.5μ in long axis smooth or with faint traces of granulation or spinulosity in the walls."

[1] Refers to Klincksieck and Valette, Code des Coleurs, 1908 (Paris).

Although the species *Penicillium olsoni* Bainier and Sartory is accepted as valid, the possibility that it represents little more than a coarse, deep variant of *P. herquei* of the same authors should be recognized.

Penicillium novae-zeelandiae van Beyma, in Antonie van Leeuwenhoek **6:** 273–275, fig. 7. 1939–1940.

Van Beyma's description as follows (abstracted):

Colonies on beer-wort agar in petri dishes after 20 days, large, about 4 cm. in diameter, consisting of numerous black sclerotia arranged in beautiful zones which are soon overgrown by delicate white, wooly mycelium becoming 2–3 mm. in depth, and showing definite funiculose ropes of hyphae; without odor; color in reverse not stated. Conidiophores rarely branched, about 500μ long, 3.0 to 3.3μ in diameter with walls conspicuously roughened, producing 3 to 5 metulae, clavate, 8 to 10μ long by 3 to 4μ in diameter, each bearing 2 to 4 sterigmata, smooth, up to 10μ long by 2.5 to 2.7μ in diameter with short tubes; conidia globose, smooth, colorless, 2.3 to 2.7μ in diameter in long chains, often diverging; conidia showing connectives; sclerotia numerous, black, mostly ellipsoid 400–800 x 300–500μ with leathery to coriaceous wall consisting of dark brown to greenish black polygonal cells.

The species was isolated by J. C. Neill of New Zealand from the fruit body of a Sclerotinia and was reported as C.B.S. 684. Its most striking character, as originally described, was production of black sclerotia in great masses and in beautiful zones in petri dish cultures.

Our notes follow:

Colonies on Czapek's solution agar growing rather restrictedly, about 2.0 to 2.5 cm. in 12 to 14 days at room temperature, irregularly furrowed, loose-textured, floccose, white to light gray, bearing scattered conidial structures within and upon a loose hyphal felt, in central colony area producing abundant black sclerotia that may become quickly overgrown and obscured by an aerial vegetative growth, occasionally showing sectors or irregular areas with abundant sclerotia accompanied by a reduced or limited mycelial development (fig. 167A); exudate limited, clear; odor lacking; reverse in dark greenish to black shades in areas of heavy sclerotial development with marginal areas in the absence of sclerotia becoming dull to fairly bright yellow to orange; sclerotia very irregular in form, usually elongate or elliptical, often confluent, with long axes oriented along radial lines (fig. 167C) usually developing in the surface of the substratum, with dimensions and texture as described above; conidial structures (figs. 167D and E) with measurements as above, but with conidiophore walls less coarsely roughened and with metulae usually in a single symmetrical verticil (as figured by van Beyma).

Colonies on steep agar spreading broadly, up to 5 or 6 cm. in 2 weeks, radially furrowed, appearing loose-textured, 2 to 3 mm. deep, comparatively

heavy sporing throughout except for a white growing margin 3 to 5 mm. wide, in gray-green shades near gnaphalium green (Ridgway, Pl. XLVII) becoming olive-gray in age; reverse black or nearly so except for narrow marginal zone; sclerotia abundantly produced, forming an almost continu-

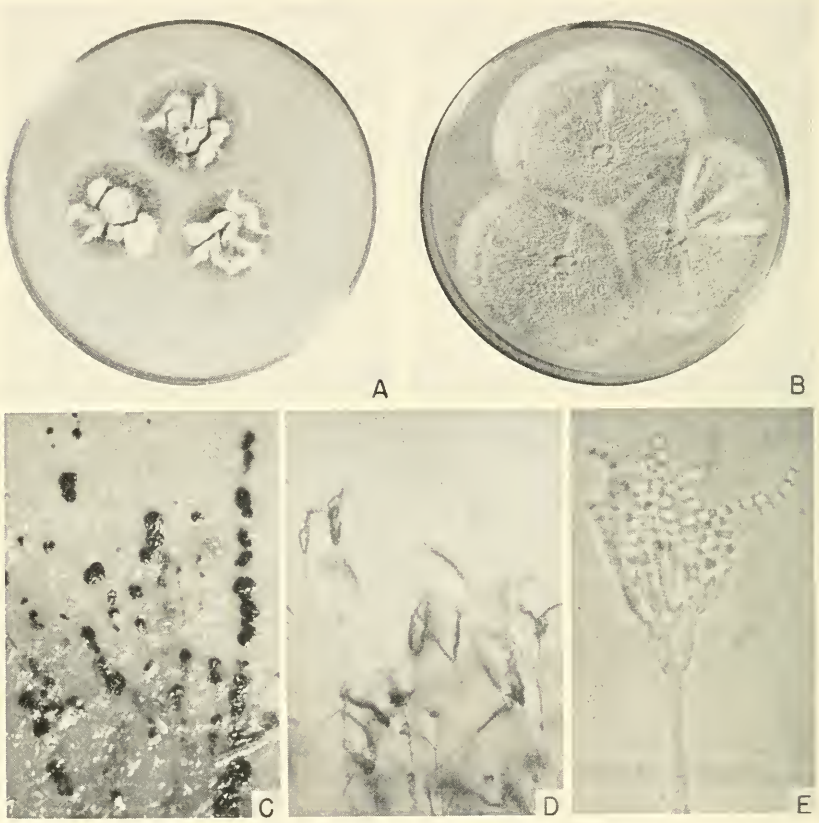


FIG. 167. *Penicillium novae-zeelandiae* v. Beyma, NRRL 2128. *A* and *B*, Two-week-old colonies on Czapek and malt agars; abundant sclerotia appear as darkened areas, particularly along inter-colony margins. *C*, Black sclerotia, largely embedded in the substratum—in this preparation superficial aerial growth has been pushed aside, × 22. *D*, Penicilli as seen at the colony margin under low power, × 80. *E*, Penicillus showing symmetrical pattern and rough-walled conidiophore, × 750.

ous coriaceous mass in the surface of the substratum throughout most of the colony area; conidial structures as on Czapek.

Colonies on malt extract agar spreading, 6.0 to 6.5 cm. in 12 to 14 days, with general texture as on steep agar but usually thinner, heavier sporing but in the same shades; sclerotia abundantly produced (fig. 166B), and concentrated along radial lines near the surface of the substratum; conidial

structures as on Czapek and steep agars but more regularly symmetrically biverticillate, and with walls of conidiophores and metulae coarsely roughened as originally described and figured.

Species description based upon van Beyma's type received from the Centraalbureau in November 1945. The species is known only from the type strain. It is maintained in our Collection as NRRL 2128.

This species was placed in Thom's section Asymmetrica-Funiculosa by van Beyma apparently upon the basis of funiculose aerial mycelium. In our cultures this character is reduced or lacking and other considerations are believed to outweigh it. The black sclerotia produced here are strikingly similar to those observed in our current study in a strain of *Penicillium funiculosum* Thom (see p. 619), and from description would seem to approximate the black sclerotia reported in *P. olsoni* Bainier and Sartory (1912). In color and general texture they are not markedly different from those occasionally observed in strains that have been accorded varietal recognition as *P. purpurogenum* var. *rubri-sclerotium* Thom. The presence of coarsely roughened and unusually long conidiophores, together with the general aspect of the cellular elements which make up the penicilli are believed to relate this species to *P. herquei* Bainier and Sartory more nearly than to any other described form. As in the latter species, the sterigmata are not strongly lanceolate, nor are conidial tubes conspicuously tapered. Nevertheless, the general pattern of the penicillus is such that we believe these forms can be found in the Biverticillata-Symmetrica more satisfactorily than in any other Section of the genus.

OCCURRENCE AND SIGNIFICANCE

Members of the *Penicillium herquei* series appear to be widely distributed but not particularly abundant in nature. They are not associated with any special substrate but are sometimes encountered in soil population studies and have been isolated from decaying vegetation, fruits, fleshy fungi, and the bodies of insects.

Although the group would seem to deserve careful investigation, since it represents one of the most colorful series of *Penicillium*, few physiological or biochemical studies are known to have been reported. Sartory and Bainier (1911b) made limited studies on the pigment of one of these molds, as did also Martini and Deribere-Desgardes (1914). No recent studies are known to us.

Chapter XIV

POLYVERTICILLATA

Colonies typically produce trailing aerial hyphae and ropes of hyphae; conidiophores arise as short septate branches; penicilli are typically polyverticillate and usually symmetrical, producing compact masses; conidia are strongly elliptical, often adherent in long chains and not forming a slimy mass.

The Polyverticillata represent a very limited group of uncertain relationship: morphologically they seem to be somewhat intermediate between *Penicillium* on the one hand and *Scopulariopsis* on the other. Biourge put them in his section Anomala along with *Penicillium brevicaule*, or *Scopulariopsis*, with which he reported them as sharing the biochemical character of emitting arsene when arsenic in any form was present in the substratum. Bainier regarded them as a section, or subgenus, in *Penicillium*, to which he assigned the name *Synpenicillium*. This had been given by Costantin, in 1888, as a generic name for the species subsequently discussed by Bainier as *P. costantini* in 1906. Thaxter, apparently from the literature, regarded some of them as species of *Gliocladium*.

Over a period of years we have seen several strains in culture which comply closely enough with descriptions given by Bainier to justify a belief that a fairly homogeneous series of polyverticillate forms exist in nature. We are not certain, however, as to the correct genetic or natural relationships of these forms. The conidial structures developed, while usually large and complexly branched, are at least strongly suggestive of many Penicillia. At the same time, the very short, thick conidiophores, the closely compacted cellular elements of the penicillus, and the not infrequent development of inverted and appressed cellular elements, or branches, toward the base of the conidiophore are strongly suggestive of species such as *Scopulariopsis costantini* (Bainier) Dale (1914). Furthermore, the conidia, while strongly elliptical, are somewhat flattened or truncate at the basal end. The Polyverticillata may, in fact, belong more with *Scopulariopsis* than with *Penicillium*. We believe it expedient, however, to recognize these forms as constituting a fourth major section within the latter genus. Workers encountering them will be immediately struck by the penicillate pattern of their conidial structures, hence will seek to locate them within the genus *Penicillium*.

Bainier (1906 and 1907) described four species which would seem to be assignable to such a polyverticillate section. Unfortunately, his descrip-

tions were very meager, and his illustrations were idealized to such a degree as to preclude positive reidentification of his forms by subsequent investigators.

While we are by no means certain of our identification, we have recently examined a culture isolated in 1940 by P. H. Waring Webb from decomposing chicken feathers at Beltsville, Maryland, which we have provisionally diagnosed as *Penicillium albicans* Bainier. Whether or not our diagnosis is correct, a discussion of this strain, together with illustrative photographs, will enable us to present the general morphology which is regarded as characteristic of the Polyverticillata.

Penicillium albicans Bainier, in Bul. Soc. Myc. France **23:** 18, Pl. V, figs. 8 and 9. 1907; Thom, The Penicillia, p. 495, fig. 87. 1930.

Colonies spreading broadly but growing very sparsely upon Czapek's solution agar at room temperature, up to 5 to 6 cm. in two weeks, *very thin*, with vegetative mycelium limited and almost wholly submerged, uncolored, lightly sporulating throughout; conidiophores arising partly from submerged hyphae, partly from trailing aerial hyphae which occasionally collect into delicate ropes, usually short, about 20 to 35μ but sometimes longer, of variable diameter up to 5 or 6μ, smooth-walled with content often appearing granular or globular; penicilli variable in form and dimensions, occasionally large and several times rebranched, but often fractional and consisting of few and irregularly arranged cellular elements.

Colonies on steep agar fairly luxuriant (fig. 168A), attaining a diameter of 5.0 to 6.0 cm. in 10 to 14 days at room temperature, with vegetative mycelium largely submerged but supporting abundant and conspicuously funiculose aerial growth, heavily sporing throughout, at first white to light cream, in age becoming light buff or even showing pale avellaneous shades, particularly in the mycelial growth and sporulating areas adjacent to the substratum; odor lacking; exudate not produced; reverse in deep tan to light brown shades; conidial structures abundantly produced, borne primarily upon short conidiophores arising from aerial hyphae and ropes of hyphae; conidiophores variable in length but mostly very short, about 20 to 40μ, typically consisting of a few short thick cells up to 6 to 7μ in diameter, smooth-walled; penicilli variable in size and pattern, commonly very large and 3 or 4 times branched below the sterigmata, often but not consistently symmetrical, with cellular elements closely appressed to form a very compact fruiting head (fig. 168B and C). Branches variable in form and size, usually becoming smaller at successive levels away from the main axis; metulae not readily distinguishable from the uppermost branches, about 8 to 10 x 2.5 to 3.0μ; sterigmata about 6 to 7μ by 2.0μ with conidium-

bearing tips somewhat narrowed; conidia strongly elliptical with basal ends somewhat flattened, about 4 to 5μ by 2.0 to 2.5μ, smooth-walled, remaining adherent in long chains in fluid mounts.

Colonies on malt agar growing very restrictedly with vegetative mycelium

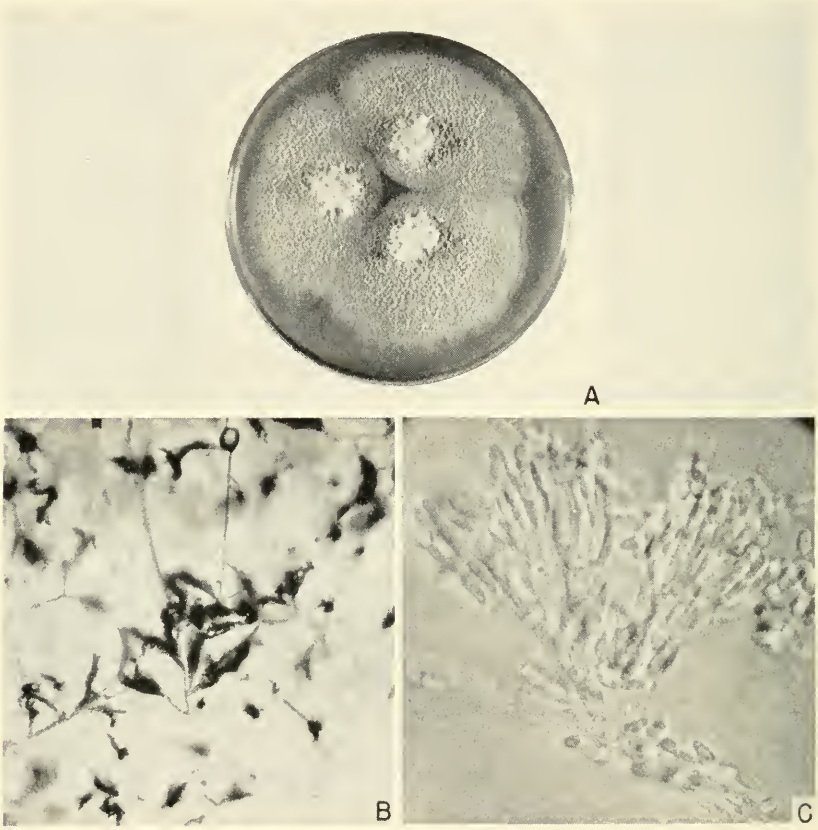


FIG. 168. *Penicillium albicans* Bainier, NRRL 1212. *A*, Colonies on steep agar at ten days. *B*, Penicilli as seen under low power, × 90. *C*, Detail of same, showing characteristic short conidiophores and compact rebranched penicilli which are sometimes 4 to 6 times verticillate below the sterigmata, × 750.

largely submerged, bearing few conidial structures but these similar to the above.

Upon steep agar, and to a lesser degree on other substrata, the submerged mycelium is characterized by the production of large, oval, smooth, heavy-walled cells, or chlamydospores, measuring about 8 to 10μ in diameter. These may be borne terminally upon short branches or in short chains up to

3 or 4 in number. Occasionally they are produced aerially. Superficially they suggest the chlamydospores, or macrospores, often seen in strains of *Paecilomyces*. On the other hand, their appearance is not unlike that of the large smooth conidia developed by species of *Scopulariopsis*, but differ from these in being produced in very limited numbers and usually within the substratum rather than upon aerial conidiiferous cells. Van Beyma (1937) described a species of *Scopulariopsis*, *S. diversispora*, which regularly produces strongly elliptical conidia in long aerial chains and at the same time globose conidia in short chains adjacent to the mycelium.

Descriptive notes are taken from strain NRRL 1212, isolated by Webb in 1940 and provisionally identified as *Penicillium albicans* Bainier.

Penicillium albicans was described by Bainier approximately as follows:

Conidiophores figured as short perpendicular branches from trailing hyphae, much larger in diameter than the sterile hyphae, consisting of 1 or 2 swollen cells, bearing a penicillus figured as regularly 2 to 3 verticillate with elements coarse, short, vesiculose rather than tubular, successively smaller in diameter, and with occasional branches directed backward from the upper cell of the conidiophore or the first verticil of branches; conidia oval, at first white then slowly fawn to reddish in age. Conidia were described as oval and a little smaller than in *Penicillium rubescens* Bainier, which had been previously reported (1906) as elliptical and 2.8 to 5.6μ in long axis.

Bainier described three additional species that are believed to be closely related to *Penicillium albicans:*

Penicillium niveum Bainier (Bul. Soc. Mycol. France **22:** 134; Pl. IX, figs. 1–4. 1906) was described with very large penicilli 5 to 7 times verticillate and with conidia strongly elliptical measuring 8.4–11.2μ by 2.8–3.0μ. The species was essentially colorless.

Penicillium insigne Bainier (Bul. Soc. Mycol. France **22:** 134; Pl. IX, figs. 5–12. 1906) was described in considerable detail with particular attention to cellular relationships within the penicillus; conidiophores ranged from very short and thick up to 280μ by 11μ. The penicillus was reported to be compact and apparently thrice verticillate; sterigmata were gradually narrowed to the apex and varied in length from 8.4 to 11.2μ; conidia were oval to oblong and were commonly 2.8 by 5.6μ.

Penicillium rubescens Bainier (Bul. Soc. Mycol. France **22:** 207; Pl. XI, figs. 7–13. 1906) was described in terms almost identical with those cited above for *P. albicans* except conidial areas were reported to range up to 5 mm. deep and to become a reddish or rusty color. Penicilli were reported as 3 to 6 times verticillate and more or less symmetrical. Conidia were reported as elliptical, 2.8 by 5.6μ, becoming rose then brownish red in ripening to produce the characteristic colony color.

It is possible that the species *Penicillium lavendulum*, recently described by Raper and Fennell (1948), may represent something of the same type of fungus as that reported by Bainier as *P. rubescens*. We believe, however,

that *P. lavendulum* is clearly distinct since it normally produces long rough conidiophores of a cellular pattern clearly different from that described by Bainier, or of that seen in *P. albicans* as we have studied the latter species. In fact, the development of strongly elliptical spores and the elaboration of a rose to vinaceous color on certain substrata (e.g., malt extract agar) constitute the only bases upon which identity of *P. rubescens* and *P. lavendulum* might be claimed.

Chapter XV

GLIOCLADIUM, PAECILOMYCES, AND SCOPULARIOPSIS

Link, in 1809, described the conidial apparatus of *Penicillium* as arising from septate branching mycelial hyphae as follows: "fertilibus erectis apice penicillato," or roughly translated, as erect hyphae with apex branched to form a little brush or broom. Saccardo, in the Sylloge (IV, p. 78, 1886) inserted before "fertilibus" the following, "inaequaliter verticillato-ramulosae." This enlargement would include any fruiting branch that one could call, loosely, a brush or broom as seen with magnification. Link, in 1816, described *Penicillium roseum* which is now regarded as a *Gliocladium*, and certain species now known to belong in *Cladosporium* were also brought in. Saccardo, as t.893 in his Fungi Italici (1877–1886), introduced *Penicillium brevicaule*, which subsequently was used as the type species of the genus *Scopulariopsis*. Thom, in 1910, described *P. divaricatum*, now assigned to Bainier's genus *Paecilomyces*.

By the time Thom published his Monograph in 1930 sufficient information was available and enough cultural material was at hand to attempt an evaluation of the genera *Gliocladium*, *Paecilomyces*, and *Scopulariopsis*. Each was regarded as distinct from *Penicillium* and from each other. Yet all were regarded as more or less related. In all of these genera, the fundamental morphological unit is the conidium-bearing cell, the *sterigma* of most authors, or the *phialid* of Vuillemin. This cell cuts off asexual aerial spores, or *conidia*, from its apex successively, *i.e.*, always with the newest spore attached directly to the sterigma and the oldest at the outer end of the unbranched chain. This eliminates all forms such as *Cladosporium* with branching chains in which the youngest spore is at the tip of each chain.

Among these molds, which are often mistaken for Penicillia, are three well defined groups. Of these, *Gliocladium* is believed to be probably most closely related, although no ascosporic stage has been available for study. The other genera, *Paecilomyces* and *Scopulariopsis* are believed to be further removed genetically. Based upon the character of the ascosporic structures produced, one can reasonably assume that *Paecilomyces* is more primitive, and *Scopulariopsis* more advanced than *Penicillium*. In the former case, asci are borne naked and singly upon short branches from fertile hyphae without any obvious development of a perithecial structure. Such ascosporic strains are referred to Westling's genus *Byssochlamys* (1909), which he regarded (and probably correctly so) as transitional

between the *Endomycetaceae* and the *Gymnoascaceae*. In the case of *Scopulariopsis*, small dark- to black-walled ascocarps are developed and these are usually, if not consistently, ostiolate. Emmons and Dodge (1931) and others have assigned such ascosporic forms to Zukal's genus *Microascus* (1890).

Corda described *Gliocladium* in 1840. Saccardo called it a true *Penicillium*. With the advent of laboratory cultivation of molds, *Gliocladium* was put back among the definitely separable genera, whose conspicuous character is the breaking up of conidial chains to form a mucilaginous mass or globule with the conidia suspended or enveloped in abundant slime which possibly arises from the liquefaction of the outer spore walls.

Bainier, in 1907, separated *Paecilomyces* as a genus with colonies never green, and with sterigmata showing spore-producing tubes usually set at a rather conspicuous angle from the axis of the cell.

In the same year, he separated *Scopulariopsis*, with Saccardo's *Penicillium brevicaule* as the type species, as a second genus which was never green and with sterigmata sloping gradually from base to conidium bearing apex and variously produced upon the fertile hyphae.

While great numbers of strains in these three groups have been seen and many specific names have been proposed by different workers, no adequate taxonomic study of either genus is available.

All three groups are constantly encountered wherever Penicillia are isolated from natural substrata, and their Penicillium-like masses of conidia are frequently assumed to belong to *Penicillium*. Hence they will be sought among the Penicillia. For this reason a brief consideration of each genus will be given, and one or more of its representative species discussed in some detail.

Gliocladium

Gliocladium of Corda, as interpreted in descriptive literature, includes species whose conidial apparatus is so Penicillium-like that they could readily be assigned to *Penicillium*, as well as species which diverge in morphology sufficiently to justify generic segregation. In the forms commonly isolated and studied by us, colony habit and appearance usually diverge fairly widely from the usual Penicillia. No consistent effort to cover all of the *Gliocladium* literature has been made, however, enough will be presented to exhibit the contrasts between the two genera. Certain species, some of which have been described and more or less commonly regarded as Penicillia, and others obviously related but seldom if ever regarded as Penicillia, will be considered.

Gliocladium Corda, in Icones Fungorum **IV:** 30–31, Taf. VII, fig. 92. 1840.

Type species *G. penicilloides* Corda, *ibid.* Latin description repeated

in Icones V: 14. 1842, with a brief paragraph in German. See also Matruchot, in Rev. Gen. Bot. **7:** 321, Pl. 16. 1895; Bainier, in Bul. Soc. Mycol. France **23:** 111–112, Pl. XV. 1907; and Thom, The Penicillia, pp. 498–510. 1930.

The essential characters given by Corda were: Conidiophores erect septate, penicillately branching above, with branches and branchlets septate, appressed, forming a solitary gelatinous head; conidia unicellular, borne upon the tips of branchlets and held together by mucilaginous substance in a dense mass.

Gliocladium was thus described as reproducing the growth habits, mycelium, conidiophores, and conidial apparatus of *Penicillium*, except that the conidia borne successively from the tips of sterigmata become enveloped in mucilaginous drops which increase in size with the increased numbers of conidia. The masses upon adjacent sterigmata fuse, then these masses fuse with those from adjacent penicilli, often forming large balls of conidia enveloped in slime (fig. 170C).

Matruchot (1895) has described perithecia and ascospore formation in certain species but, insofar as we know, this has not been confirmed by others. The forms constantly encountered in our cultures are purely conidial. Comparative studies of structure in both conidial and ascosporic forms (if refound) will be necessary before *Gliocladium* and *Penicillium* can be safely placed with reference to each other among the Ascomycetes.

Corda, in his Prachtflora (1839), also described as *Clonostachys araucaria* (see p. 18) a penicillate organism which he figured as producing columns of elliptical conidia with the long axes of the conidia diagonal to the axis of the column. That is, the conidia forming the column were adherent side by side instead of end to end as in *Penicillium*, or enveloped in slime as in *Gliocladium*. There are reasons for believing that *C. araucaria* approaches fairly closely some forms ordinarily assigned to *Gliocladium roseum*.

In the description of *Gliocladium*, the character most emphasized is the envelopment of conidia in balls of slime. The conidial apparatus as observed and figured is superficially Penicillium-like, especially in material washed in alcohol and mounted for examination, and similar forms have been placed sometimes in *Penicillium* and again in *Gliocladium*. Few attempts to establish real relationships have been recorded. The primary branching system varies from asymmetrical to symmetrical with many of the described species approaching the repeated and usually symmetrical branching system of the polyverticillate Penicillia (see p. 668) but differing markedly from these in the character of conidiophores, cellular elements and conidial masses. The diameter of the main conidiophore is usually greater than that of the primary branches, and the elements in each succeeding stage of branching are usually smaller. The sterigmata vary from

shapes and measurements of those in typical Penicillia to long subulate tubes. In some species, as also in the polyverticillate, a series of reflexed or "rhizoid"-like branches often forms a claw-like support at the base of the conidiophore.

From the standpoint of relationship with *Penicillium*, the process of conidium formation becomes significant. The typical cell of the group is the sterigmata which cuts off conidia from its apical tube. Microscopic examination shows that the conidia are cut off successively from the tips of sterigmata just as they are in *Penicillium*, but typically do not adhere in chains. Instead they slip back and become enveloped in slime. In studying various areas and different ages of petri dish colonies of certain strains, transitional steps are found. In some areas the conidia remain for a time in chains, in other areas of the same colony penicilli show the Clonostachys-type of conidial columns in which the conidia are arranged diagonally and in still other areas the conidia are found massed in the typical slime balls.

Correlation of these observations with cultural conditions shows the Penicillium-like arrangement of conidia to be primitive and regularly present in conidial structures during the process of conidium formation. One species, *Gliocladium vermoesenі* (Biourge) Thom, produces separate chains of conidia that retain their identity as in *Penicillium*. In another species, *G. catenulatum* Gilman and Abbott (1927), the conidia may remain end to end in chains, but the chains become adherent into enslimed columns bound more firmly than in any of the true Penicillia (fig. 170B). In *G. deliquescens* the conidial apparatus is regularly penicillate, but the conidia invariably accumulate into conspicuous balls of abundant slime (figs. 170C and D). The extent of the deliquescence thus determines whether conidia in several chains will remain in position as produced, or will adhere into wet columns as figured by Gilman and Abbott for *Gliocladium catenulatum*, or whether every conidium will slip back slightly toward the base of the chain to assume a position diagonal to the axis of the column, as in *Clonostachys*, or whether no cell-to-cell relationship will be maintained and all conidia will collect into a composite globule of slime in the manner regarded as typical of the genus *Gliocladium*.

Three more or less contrasting series of *Gliocladium* are commonly encountered in culture, namely:

(1) *Gliocladium roseum* series. This rosy or salmon series shows a fairly complete gradation from forms near *G. vermoesenі* (Biourge) Thom with conidial structures like a true *Penicillium*, through types simulating Corda's *Clonostachys araucaria* with the end-to-end relations of conidia broken and each cell slipped half its length backward, to forms like *G. roseum* in which the slime balls are usually well established.

(2) *Gliocladium catenulatum* series. A predominantly floccose series in which the colonies show abundant radiating floccose or funiculose aerial hyphae and produce abundant green masses of conidial structures distributed in characteristic manner. The series is typified by *G. catenulatum* Gilman and Abbott, in which the conidia may either remain in chains which adhere into wet columns or form slime balls wholly typical of the genus.

(3) *Gliocladium deliquescens* series. A dark green to fuscous series, represented by such forms as *G. deliquescens* Sopp which is common in soil, and which develops a widely spreading, submerged mycelium on Czapek agar with scattered areas or clumps of conidial structures above the surface. The conidia of these forms regularly collect into conspicuous slime balls.

The more common and easily recognized members of the genus *Gliocladium* may be separated as shown in a simple key, as follows:

Page

I. Conidial areas colorless, cream-colored or in salmon to rosy pink shades. *G. roseum* series 677

A. Conidia colorless, cream, or pale pink in color, wholly or in part collecting into slime balls ..... *G. roseum* (Link) Bainier 678

B. Conidia in rosy pink to vinaceous pink shades, usually remaining adherent in chains ..... *G. vermoeseni* (Biourge) Thom 680

II. Conidial areas in pale yellow-green to dark green shades.

A. Conidia typically in pale yellow-green shades, commonly remaining in chains to form wet columns ..... *G. catenulatum* series 682

G. catenulatum Gilman and Abbott 682

B. Conidia typically in dark green to almost black shades, always collecting into slime balls ..... *G. deliquescens* series 686

G. deliquescens Sopp 686

Gliocladium roseum Series

Type Species: *Gliocladium penicilloides* Corda, in Icones Fungorum **IV:** 31, Taf. VII, figs. 88 and 89. 1840.

Corda described mold colonies found fruiting upon the hymenial surface of rotting *Thelephora* with the following characters: Colonies small, white; conidiophores erect, flexuous, enlarging above, septate, pulverulent, colorless; penicillus with primary branching opposite, branchlets verticillate in fours, appressed; heads of conidia globose, white; conidia 6μ in long axis, oblong, embedded in a mucilaginous mass.

By this description, as pointed out by Gilman and Abbott (1927), the type of the genus falls in the non-green section—with the type species, *Gliocladium penicilloides*, designated white by Corda. As seen in cultures, many gradations from white to rosy, pink, or salmon shades can be found.

These forms are common in nature and representatives of the series have found their way into many collections. One of them was discussed by Thom in 1910 as *Penicillium roseum* Link. The substitution of the name *Gliocladium* for *Penicillium* was first suggested by Bainier (1907). The description of Thom's form, which is representative, and notes as to its distribution, follows:

Gliocladium roseum (Link?) Bainier, in Bul. Soc. Mycol. France **23:** 111–112, Pl. XV, fig. 1–6. 1907.

Probable Synonym: *P. roseum* Link, in Obs. II, p. 37, 1816; see also Link, in Sp. Plant Ed. 4, Vol. 6, pt. 1, p. 69, 1824; Fries, in Sys. Myk. 3, p. 409, 1829; Persoon, in Myc. Europ. 1822; and Thom, in U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, p. 49, fig. 15, 1910.

Colonies on all common media growing rapidly (fig. 169A and B), white to pink or salmon in fruiting areas, aerial mycelium loosely floccose or funiculose, with simple hyphae and ropes of hyphae irregularly producing colorless, through cream to pinkish masses up to 1 mm. or more deep in old cultures; conidiophores borne as perpendicular branches from aerial hyphae or ropes of hyphae, 45 to 125μ in length (fig. 169C); penicilli up to 140μ in length, irregularly once- or twice-branched alternately or verticillately (fig. 169D), with sterigmata varying from 12μ by 2.0 to 3.0μ in verticils of 5 or less to 17μ by 2.3μ when solitary, bearing conidia which typically become aggregated into gelatinous balls or masses; conidia colorless (sometimes pink or rosy in mass), elliptical, 5 to 7μ by 3 to 4μ, slightly apiculate, smooth, appearing delicately granular within.

Thom's strain was bought from Kral, in Prague, Bohemia. Closely similar organisms have been commonly isolated in this Laboratory, or received from correspondents in this country and abroad. A specimen under the name *Penicillium roseum* Link, as No. 1179 in DeThümen's Mycotheca Universalis, collected by Ravenel in South Carolina in 1876 upon leaves of *Buxus*, is contained in the mycological collections of the Bureau of Plant Industry, United States Department of Agriculture. The number of specimens found under the name *P. roseum* Link from widely scattered workers appears to justify the belief that the above form represents the type of organism described by Link under this name.

Since the development of a mucilaginous mass enveloping the conidia has come to be regarded as sufficient basis for separation of species under the generic name of *Gliocladium*, the species should become *Gliocladium roseum* (Link), as reported by Thom in 1930. Bainier (1907) independently, and without reference to Link, described a new species as *Glio-*

cladium roseum which undoubtedly belongs here. There is some question, however, as to complete identity of Link's and Bainier's species.

Under strict interpretation of generic definitions we have seen in single cultures of *Gliocladium roseum*, fruiting structures determinable as *Penicillium*, *Gliocladium*, and when old, *Clonostachys*.

FIG. 169. *Gliocladium roseum* series. *A* and *B*, Ten-day-old colonies of NRRL 1085 on Czapek and malt agars. *C*, Low-power view of inter-colony area, × 85. *D*, Detail of penicillate conidial apparatus, × 750.

Bainier's type of *Gliocladium roseum* is maintained in our Collection as NRRL 1084. NRRL 1085, isolated from soil in 1930, is also representative.

The following species are assignable near *Gliocladium roseum* (Link) Bainier, if indeed they are not synonymous with it.

Gliocladium penicilloides Corda, in Icones Fungorum **IV:** 31; Taf. VII, figs. 7 and 8. 1940. See also Gilman and Abbott, in Ia. State Col. Jour. Sci. **1:** 303. 1927; and

Thom, The Penicillia, p. 504. 1930. It is now impossible to know just what type of mold Corda had at hand when he described *G. penicilloides* except that it was verticillately branched and colorless, and that the conidia collected into a mucilaginous mass. In their Summary of Soil Fungi, Gilman and Abbott (1927) gave conidia as elliptical to bacillate, smooth, 3.5–4.0μ by 2.0μ. These measurements are definitely less than those observed in cultures which we have assigned to the *G. roseum* series, and provisionally regard as probably representing *G. roseum* (Link) Bainier. Strains ranging all the way from almost sterile to heavily sporing and from wholly colorless to pale rosy pink (approaching but not reaching *G. vermoeseni*) have been examined, and it is our general observation that the amount of color correlates fairly closely with the quantity of conidia produced. We have not observed marked differences in the dimensions of conidia. Careful comparative studies will be needed to determine whether a satisfactory line of separation can be established between *G. penicilloides* and *G. roseum*. We are led to believe that the two merge insensibly into each other, and that the former probably represented merely a colorless or lightly colored form of the latter species.

Acrostalagmus roseus Bainier, in Bul. Soc. Mycol. France **21**: 225–227, Pl. XII, figs. 1–9. 1905. Conidial structures described as verticillately branched; sterigmata in verticils of 3 to 5 and measuring 16μ by 2.0μ; conidia rosy *en masse*, ovoid to globose 2.0 to 6.0μ by 2.0 to 3.0μ, becoming embedded in a mucilaginous mass.

Isaria clonostachoides Pritchard and Porte, in Phytopathology **12**: 167–172, Pl. XII and fig. 1. 1922. This coremiform fungus bearing enslimed masses of pink to pale salmon colored conidia probably represented one of the *Gliocladium roseum* series.

Gliocladium vermoeseni (Biourge) Thom, in The Penicillia, pp. 502–503. 1930.

Synonym: *Penicillium vermoeseni* Biourge, in Monogr., La Cellule **33**: fasc. 1, p. 230, Pl. XXIII, fig. 137. 1923.

Described by Biourge as follows:

Colonies on wort gelatine, producing numerous salmon colored coremia 10 mm. in height or more; conidiophores about 5μ in diameter; metulae 7 to 15μ by 2.5 to 5.0μ, irregularly borne, irregular in number or none; sterigmata 10 to 20μ by 2.5 to 3.5μ, in groups of 2 to 5, or even 7; conidia elliptical 5.0 to 7.5μ by 3 to 4μ. Habitat: Certain species of *Areca* (palms) parasitic or semi-parasitic.

A culture under this name was received from Dr. Westerdijk in 1926 and noted by Thom (1930) as having two forms of conidia, a rosy form and a green form. The two forms were readily separated, and the rosy form was compared with Biourge's discussion of *Penicillium vermoeseni*. There was good reason to believe this to be Biourge's organism and probably his type strain transmitted through several workers. The following description is based upon our cultures of this strain.

Colonies on Czapek's solution agar, broadly spreading, covering the entire surface of the substratum in petri dishes within 8 to 10 days, loosely

floccose, surface uneven, white becoming salmon to rosy pink with the development of ripe conidial masses; odor evident, peculiar; reverse colorless, then yellowish to yellowish pink; hyphae sinuous, colorless, coarse, 3 to 6μ in diameter, showing large and numerous vacuoles; conidiophores mostly as short branches from trailing interlacing aerial hyphae and ropes of hyphae, about 100 to 200μ by 4 to 5μ; conidial apparatus variously produced, partly as single sterigmata borne as terminal cells on short branches, but usually composed of irregular branching systems and oftentimes truly penicillate, forming irregularly distributed conidial masses, at first white then salmon or rosy; metulae when recognizable 10 to 12μ by 3μ at base and with apices enlarged; sterigmata very irregular in size, commonly 8.0 to 12μ but sometimes up to 20μ or more when borne singly; conidia 4 to 6μ by 3 to 4μ, colorless, somewhat irregular at first, elliptical when ripe, forming chains 1 to 2 mm. in length in old cultures and often adhering in large masses which break off.

Despite the fact that the conidia remain in chains, the conidial apparatus found here allies this species closer to *Gliocladium* than to *Penicillium*, hence the present allocation.

Gliocladium vermoeseni (Biourge) Thom is believed to represent an extreme type in the variable *G. roseum* series. Once seen it is easily recognized because of its distinctive coloration, the general aspect of its conidial apparatus, and the tendency to produce conidia in chains as in *Penicillium* rather than in slime balls as in the more typical species of *Gliocladium*.

The species is represented by NRRL 1752 from H. S. Fawcett and two strains received under this name from the Centraalbureau in December 1946 as isolates from infected palms.

Occurrence and Significance

Members of the *Gliocladium roseum* series are abundant in soil and on decaying vegetation of many types. They have been commonly isolated from exposed fabrics and other items of military equipment. Occasional strains appear to be fairly active cellulose decomposers.

Gliocladium roseum and *G. vermoeseni* are commonly reported to be parasitic or semi-parasitic on ornamental plants. Miss McCulloch and others in the Department of Agriculture in Washington, D. C. have reported extensive losses in *Buxus* (boxwood) due to *G. roseum*. *Verticillium buxi* was also reported to be present. Dodge (1944) has carefully investigated the different fungi associated with leaf and twig diseases in *Buxus* and pointed out the interrelation of such commonly reported forms as *Volutella buxi*, *Verticillium buxi*, and *Penicillium roseum* and concludes that the latter is less commonly present than generally reported. As early as 1859, Berkeley and Broome had cited *P. roseum* as occurring on *Hibiscus*. Klotz

(1931) reported *P. roseum* to be a wound parasite capable of infecting harvested dates.

Biourge based his species *Penicillium vermoeseni* upon a fungus isolated in Belgium from certain species of *Areca* (palms) grown under glass. Bliss later (1935) isolated the same species from various types of diseased palms in California, and in a more detailed communication subsequently (1938) reviewed the occurrence and seriousness of such infections as they had been reported by Robertson-Proschowsky (1924), Fawcett (1930), and other investigators, usually as due to *P. roseum*. The disease was especially severe in plantings of the palm, *Washingtonia filifera*.

In the literature, differentiation between forms regarded as representing *Gliocladium roseum* and *G. vermoeseni* is usually not clear.

Gliocladium catenulatum Series

The present series appears to be intermediate between (1) the *Gliocladium roseum* series in which the conidia are colorless to flesh or rosy pink, and which may be borne in well-defined chains and (2) the *G. deliquescens* series in which the conidia are dark green, and which regularly collect in balls of slime typical of the genus. In the *G. catenulatum* series, conidia are mostly pale yellow-green in color and may either remain in chains to form wet columns (fig. 170B), or collect into typical slime balls. Colonies in this series are usually deeply floccose and show considerable ropiness (fig. 170A). Conidial development begins late and is most abundant in colony centers and sometimes in outlying concentric zones (fig. 170A). One species, *G. catenulatum* Gilman and Abbott, can be easily recognized, and may be regarded as typifying the series. Another species, *G. fimbriatum* Gilman and Abbott, may belong here, but cultures distributed as type seem to place this in another genus (see discussion below).

Van Beyma's *Gliocladium flavum*, described in 1928, has not been available for study but from the description and figures it would appear to belong in the present series.

Gliocladium catenulatum Gilman and Abbott, in Ia. State Col. Jour. Sci. **1:** 303, fig. 37. 1927.

Gilman's and Abbott's diagnosis follows:

"Colonies on Czapek's agar pure white, spreading, floccose, becoming olive green to bright green in the center as fruiting areas develop, and clear dark green in old cultures; fruiting areas are usually confined to center of colony and one or two concentric zones separated by sterile mycelium; reverse colorless to yellowish. Aerial mycelium abundant, simple or in ropes, from which the conidiophores arise as branches. Conidiophores often once and sometimes twice branched, coarse, pitted

or rough, 50 to 125μ long. Heads are composed of conidial chains in long, close columns, enveloped in slime, up to 150μ long. Fructification in three stages, elements of fructification pitted or rough; primary branches 15 to 20μ by 3.5 to 4.0μ; metulae 7 to

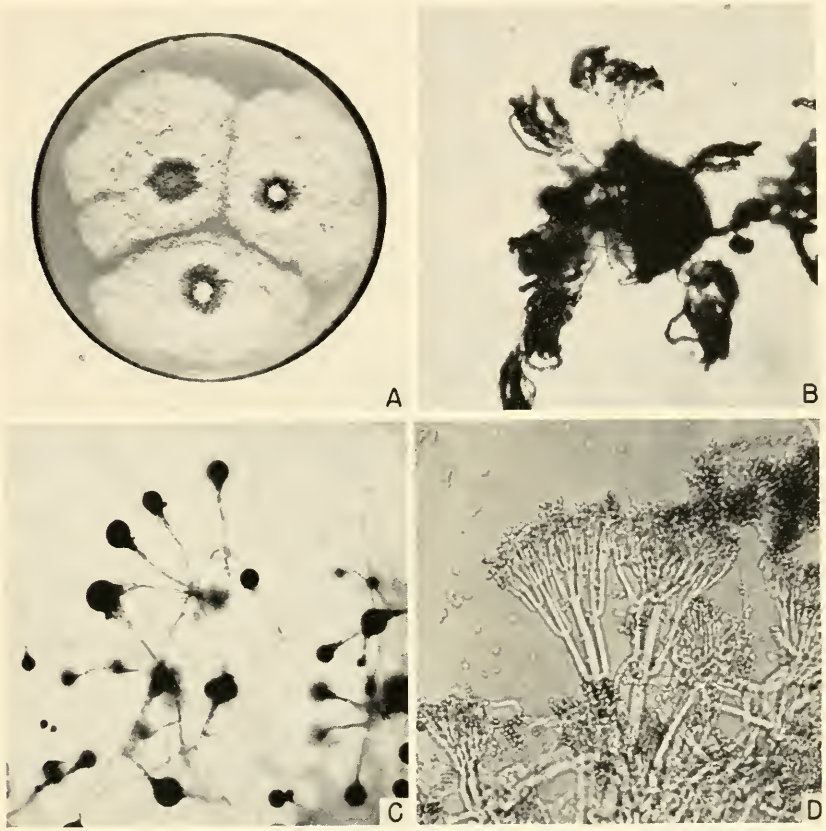


FIG. 170. *Gliocladium* Corda. *A*, Ten-day-old colonies of *G. catenulatum* Gilman and Abbott, NRRL 1091, on Czapek agar. *B*, Conidial structures as seen under low magnifications, × 90; note the columns of enslimed conidia. *C*, *G. deliquescens* Sopp, NRRL 1086, as seen on Czapek agar under low magnification, × 80. *D*, Enlarged view of similar conidial structures, × 250; note progressively smaller dimensions of cellular elements from the conidiophore outward.

9 by 15 to 25μ; phialides 10 to 20μ long. Conidia elliptical, smooth, pale green, 4.0 to 7.5μ by 3 to 4μ.

"From Soil: United States: Utah."

Our notes follow:

Colonies on Czapek's agar complying with Gilman and Abbott's description.

Colonies on steep and malt agars as on Czapek but growing somewhat more rapidly and often sporulating less abundantly and more tardily; reverse developing pale yellow to rosy cream shades.

Conidial structures are in general agreement with the describer's diagnosis and often develop the wet spore columns described. On the other hand, they commonly show conidia collecting into characteristic balls of slime. Conidiophores appear roughened when viewed dry under low power, but in liquid mounts under oil usually appear smooth.

The species appears to be fairly common in soil. NRRL 1091 and 2158 are representative.

Gliocladium fimbriatum Gilman and Abbott, in Ia. State Col. Jour. Sci. **1:** 304, fig. 38. 1927, was described as follows:

"Colonies on Czapek's agar broadly spreading, orbicular, pure white at first, with zones of dark leaf green fruiting areas appearing near the center of the colony. Conidiophores arise from aerial hyphae, smooth, up to 25μ long; several from one point, stolon-like hyphae usually present at point of origin. Heads enveloped in round balls of slime in which chains are not distinguishable; fructification in two stages, with divergent branchlets or metulae which bear elongate flask-shaped, appressed phialides, or with conidia borne directly on a few finger-like phialides which arise irregularly from the conidiophores; in most heads one or more branchlets arise laterally from the conidiophore some distance below the main head; metulae elongate, extremely variable in size, phialides usually 10 to 20μ long, from flask-shaped to irregular elongate. Conidia elliptical or elongate, ovoid, smooth, pale green, 6.5 to 9.5μ by 2.5 to 4.0μ.

"From soil: United States: Iowa, Louisiana."

Much has been written about this latter species, principally because of Weindling's (1932, *et. seq.*) report of the production of an antibiotic which he subsequently termed gliotoxin (1941). His culture was first regarded as a species of *Trichoderma* but, upon the advice of Timonin and Thom, was reported as *Gliocladium fimbriatum* (1937). Recently, Brian and coworkers (1944 and 1945) in England, have questioned this diagnosis and by way of supporting their view have demonstrated the production of gliotoxin by strains which they regard as unquestionably representing *Trichoderma*. Weindling's culture has been retained and today would seem to represent a species of *Trichoderma*. Under the usual conditions of culture, however, it shows conidial structures sometimes almost penicillate and conidia collecting into slime balls in the manner characteristic of *Gliocladium*, which characteristics undoubtedly furnished the bases for Thom's diagnosis.

A culture, presumably type, was received from the Centraalbureau in May 1946, as *Gliocladium fimbriatum* from Abbott in 1927. Careful examination and comparison with Pope's *Metarrhizium glutinosum* (Mycologia

36: 343–350, 2 figs. 1944) shows it to almost duplicate the latter species. Recently, White and Downing (Mycologia **39:** 546–555, 2 figs. 1947) have reported that Pope's species represented, in fact, not a *Metarrhizium* but *Myrothecium verrucaria* (Alb. and Schw.) Ditmar ex Fr. Furthermore, re-examination of Gilman and Abbott's description and figures confirms the belief that the culture from Baarn probably represents the original isolate in essentially unaltered form. Strains such as this, which would now be assigned to *Metarrhizium glutinosum*, or some species of *Myrothecium*, quickly and consistently produce conidia in slime balls and are dark green in color, hence might easily be misinterpreted as representing a species of *Gliocladium*.

In view of the above, the validity of *Gliocladium fimbriatum* Gilman and Abbott is extremely questionable and the species is omitted from the general key to the genus.

Occurrence and Significance

Gliocladium catenulatum appears to be fairly common in soil, hence is believed to contribute to slow aerobic processes of decay. Strains approximating those represented by this species were investigated by Dr. Shorey in the Department of Agriculture several years ago and found to contain substantial amounts of chitin or chitin-like substances.

As early as 1932, Weindling showed that if you grew a mold, which he identified as a species of *Trichoderma*, in the presence of certain plant pathogenic fungi, *e.g.*, *Rhizoctonia*, the growth of the plant pathogen was inhibited. At that time he did not attribute the inhibition to a particular substance. But in 1936 he and Emerson published a paper in which this antagonistic effect was attributed to a definite crystalline substance. The mold was identified as *Gliocladium fimbriatum* about this time and the name gliotoxin was later given (1941) to the active substance. Gliotoxin is soluble in chloroform and alcohol, and its structure and synthesis as worked out by Dutcher, Johnson, and Bruce has been reported in a series of papers (1943 and 1944). Gliotoxin is strongly fungistatic, and is moderately bacteriostatic. In England, Brian and associates (1944, 1945) have published some recent papers regarding antibiotics produced by species of *Trichoderma* and related forms, and have gone into the antifungal properties of these antibiotics much more thoroughly than has been done previously.

An antibiotic termed viridin, which, like gliotoxin, is highly fungistatic, has been reported from *Trichoderma viride* by Brian and co-workers (1945, 1946b). It inhibits species of *Botrytis* and *Fusarium* in comparatively high dilutions.

Glutinosin, an antibiotic produced by *Metarrhizium glutinosum* Pope, was recently reported by Brian and McGowan (1946). The substance is

not markedly bacteriostatic but is active against a number of fungi including the fruit-rotting Penicillia, *Penicillium expansum* (pomaceous fruits) and *P. digitatum* (citrus fruits).

Gliocladium deliquescens Series

This well-marked series is characterized by conidia which *en masse* appear dark green to almost black and which regularly collect in large slime balls. These may be borne upon individual fructifications or they may coalesce to form larger masses where several conidial structures arise in close proximity (fig. 170C).

The series is typified by *Gliocladium deliquescens* which was described and beautifully illustrated by Sopp in his Monograph (1912, pp. 89–93, Pl. I).

Gliocladium deliquescens Sopp in Monogr., pp. 89–93, Taf. I, figs. 1–6. 1912; Gilman and Abbott, in Ia. State Col. Jour. Sci. **1:** 304–305. 1927; and Thom, The Penicillia, pp. 507–508. 1930.

Sopp's diagnosis abstracted:

Colonies clear yellowish green becoming darker in age, at first a typical area of crowded, Penicillium-like conidiophores which later become enveloped in slimy masses as the conidial chains dissolve and run together; reverse gray at first, later dark green, almost black, odor characteristic; gelatin liquified; conidiophores up to 1 mm. long, erect, coarse, septate, 1 to 5 times penicillate branching, each series of branchlets progressively smaller so that the sterigmata are much smaller in diameter than the primary branches; conidia about 1.0 by 1.5 to 2.0μ or somewhat larger when ripe, at first fusiform, later becoming more rounded at the ends, produced in chains which break up as the conidia become enveloped in masses of slime; perithecia and sclerotia not found.

Species originally isolated from a specimen of *Daedalea unicolor* in Norway, but subsequently shown to be common in soil and on decaying vegetation by many investigators. Sopp reported colonies to grow well upon various media, and the species to remain viable for three years.

Sopp's type was not seen. Gilman and Abbott (1927) described and illustrated an organism under this name as follows:

"Growth not abundant on Czapek's agar. On bean agar, broadly spreading, producing a thin, transparent growth of sterile hyphae over the entire medium, from which the dark green fruiting areas soon develop; surface deep, dark green to blackish green; reverse colorless. Aerial mycelium scant, colony consisting almost entirely of conidiophores and slimy heads. Conidiophores arise from submerged and surface hyphae, several from one point; both aerial and submerged stolons present at these points; conidiophores 100 to 225μ by 8 to 10μ. Fructification typically in four stages, consisting of three to five primary branches arising from the apex of the conidiophore; these bear a verticil of secondary branches, and these verticils of metulae; phialides

closely crowded on the metulae, club-shaped; primary and secondary branches and metulae elongate oblong, slightly inflated at the apex. Primary branches 15 to 20μ by 3.0 to 3.5μ; secondary branches 13 to 15μ by 3 ; metulae 8 to 10μ by 1.5 to 2.0μ; phialides 6 to 8μ by 1.0 to 1.5μ. Conidia elliptical, greenish, smooth, granular within, 3.0 to 3.8μ by 2.0 to 2.5μ. Hyphae, conidiophores, and elements of fructification coarse and pitted, or rough. Slime production very abundant, usually enveloping the entire colony.

"From soil: Louisiana."

In our analyses of soil isolations, and in our searches for industrially important molds during recent years, forms obviously representing Sopp's species have been commonly encountered. These are characterized by thin, spreading, submerged colonies on Czapek agar with the development of scattered, coarse conidial structures (fig. 170C) of the type described and illustrated by Sopp. They differ from Sopp's description only in producing larger conidia, about 3.0 to 3.5μ by 2.0μ, which is in close agreement with Gilman and Abbott (1927). Conidiophore walls appear coarsely roughened when viewed dry, and smooth or nearly so in liquid mounts, but with contents showing conspicuous globular inclusions. The bright green sterigmata and conidia described and illustrated in color by Sopp are particularly striking, as are also the stolon or rhizoid-like structures described by Gilman and Abbott.

Gliocladium nigro-virescens van Beyma, in Verh. Akad. Wetens. Amst. Natuurk (Tweede Sect.) **29:** 30–32, fig. 1. 1931. This species is probably best assigned to the *G. deliquescens* series although it appears to be somewhat transitional in the direction of *G. catenulatum*. Colonies on Czapek agar are about 6.0 cm. in two weeks, floccose, white to cream, lightly sporulating and principally in the colony center. Colonies on steep agar growing more luxuriantly and heavier sporing throughout, with conidia consistently collecting into slime balls, dark green in color. Conidial structures irregular, often large, rebranched two or three times below the sterigmata; sterigmata thin, variable in length but mostly 10 to 15μ; conidia elliptical, mostly 3.5 to 5.0μ by 2.0 to 2.5μ with points of origin or attachment usually evident as in most other species of the genus.

We can only guess whether comparative study of the green Gliocladia might establish this as a clearly distinct species or show it to be a variant of some other form.

Gliocladium atrum Gilman and Abbott (Ia. State Col. Jour. Sci. **1:** 305, fig. 40. 1927) represented some dematiacious form, hence not properly assignable to *Gliocladium* despite the production of conidia in slime balls from flask-shaped sterigmata.

Occurrence and Significance

Gliocladium deliquescens is unusually abundant in most soils, hence is presumed to play some active role in decomposition processes. Occasional strains were encountered among the molds isolated from deteriorating military equipment in the field. No biochemical or physiological studies with this species are known to us.

Paecilomyces

Bainier, in 1907, established the genus *Paecilomyces*, with the type species *P. varioti*, to cover a saprophytic mold lacking green color but producing verticillately branched conidial structures superficially resembling those produced in *Penicillium*. His generic description as translated and emended by Thom in 1930 (p. 541) follows:

"Genus related to *Penicillium* and *Aspergillus*, distinguished by sterigmata short-tubular or more or less enlarged, tapering into long conidium-bearing tubes mostly curved or bent slightly away from the axes of the main sterigmatic cells; sterigmata variously arranged, partly in verticils and branching systems suggesting *Penicillium*, partly irregularly arranged upon short branchlets, partly arising singly along the fertile hyphae; conidia in chains, elliptical, never green."

Thom, in 1910, described *Penicillium divaricatum* and subsequently accumulated a large series of closely related strains. Later Bainier's strain of *Paecilomyces varioti* was received from Paris and easily seen to be identical although no one had reported its identification from Bainier's description. *Paecilomyces* was, therefore, accepted as the correct generic usage in Thom's Monograph (1930, pp. 544–545). Horne and Williamson (1923), working with an organism of this group, described as "macrospores," large cells which were borne mostly near, or just below, the surface of the culture medium upon solitary or variously aggregated branchlets from the fertile hyphae. They regarded these macrospores as fixing the generic allocation of the species and transferred it to *Eidamia* of Lindau (1907). These accessory structures were previously known to Thom but were not discussed by either him or Bainier in their original descriptions. Thom, in 1930, figured such structures and noted their abundance in certain strains, particularly in one which had come from Kita and Wai in Japan. Their significance soon became apparent when Olliver and Smith (1933) discovered a strain presenting the general morphology of *P. varioti* in all respects except that these sterile cells, or "macrospores," developed into individual asci and each produced eight smooth, hyaline, ovate ascospores measuring 6.0 to 6.5μ by 4.3 to 4.5μ. Olliver and Smith assigned their ascosporic strain to Westling's genus *Byssochlamys* (1909) as a new species, *B. fulva*. In discussing the genus *Byssochlamys*, Thom, in 1930, had observed that the conidial apparatus of Westling's species suggested relationship with *Paecilomyces*. Emmons, in his study of ascocarps of *Penicillium* (1935), discussed the details of ascospore production and contrasted this with the Penicillia. Westling regarded his genus *Byssochlamys* as intermediate between the Endomycetaceae and the Gymoascaceae, a position which it seems to fit quite well.

Diligent search over a number of years has revealed few ascosporic

strains of this genus in America, although it appears to be fairly common in England where it presents something of a problem in fruit preservation (Olliver and Rendle, 1934) since the ascospores survive the usual canning process. Olliver and Smith's strain, now maintained as NRRL 1125, still produces ascospores abundantly in our hands more than fifteen years after it was first isolated.

There appears to be little question but that *Paecilomyces varioti* Bainier and *Byssochlamys fulva* Olliver and Smith represent conidial and ascosporic phases, respectively, of the same fungus. However, since no detailed study of either genus has been made for this Manual, the authors hesitate to combine the descriptions or to recognize one species above the other. Since the conidial phase is commonly encountered in the routine examination of saprophytic molds, and since the ascosporic form may be reisolated, we present below a description of the former species taken largely from Thom (1930), and Olliver and Smith's (1933) diagnosis of the latter.

Thom, in his Monograph (1930), cited several additional species as probably belonging to the genus *Paecilomyces*, including the following:

Penicillium arenarium Shaposhnikov and Manteifel. Trans. Sci. Chem.-pharmaceut. Inst., Moscow **5:** 1–64, figs. 1923. In Russian.

Paecilomyces aureo-cinnamomeum (Biourge) Thom. See *P. aureo-cinnamomeum* Biourge, Monogr., La Cellule **33:** fasc. 1, pp. 213–214; Col. Pl. V, Cart. 61; Pl. VIII, fig. 48. 1923.

Paecilomyces burci (Pollacci) Thom, in The Penicillia, p. 548. 1930.
Synonym: *Penicillium burci* Pollacci, in Ist. Bot. d. R. Univ., Pavia, II ser., **18:** 128–129. Tav. XXXI, figs. 4–6. 1921; see also paper by Campatelli, in Pensiero med., Milano **12:** 217–219. 1923.

Corollium dermatophagum Sopp, in Monogr., pp. 99–103, Taf. X, fig. 108, Taf. XXIII, fig. 45. 1912.

Spicaria fimetaria Moesz, in Botanikai Köslemenyek **19:** 58, fig. 9 (p. 59). 1921.

Penicillium flavum El. and Em. Marchal. Bul. Soc. Roy. Bot. Belgique **54** (Ser. 2 T. IV): 129. 1921.

Paecilomyces mandshuricum (Saito) Thom, in The Penicillia, p. 550. 1930.
Synonym: *Penicillium mandshuricum* Saito, in South Manchuria Railway Company, Central Laboratory, Report no. 6, pp. 11–12. In Japanese.

P. repandum Bainier and Sartory, Bul. Soc. Mycol. France **29:** p. 367. 1913.

Of the above, *Paecilomyces burci*, *P. aureo-cinnamomeum*, and *P. mandshuricum* were regarded as possibly separable from *P. varioti*. Limited comparisons, in culture, of strains maintained in our Collection or received from Baarn, under these names, have been made and minor differences in conidial color and colony appearance have been observed. It is questionable, however, whether these differences represent more than different aspects of a very abundant and variable species.

Since the publication of Thom's Monograph, Kennelly and Grimes (1930)

have described a new species, *Paecilomyces hibernicum*, isolated from butter in Ireland. Conidia are elliptical, 4.0 by 2.6μ, and range from hyaline to pink; macrospores are reported. Thom is said to have confirmed the fungus as a new species. A strain under this name, presumably type, received in August 1946 from the Centraalbureau, now produces broadly

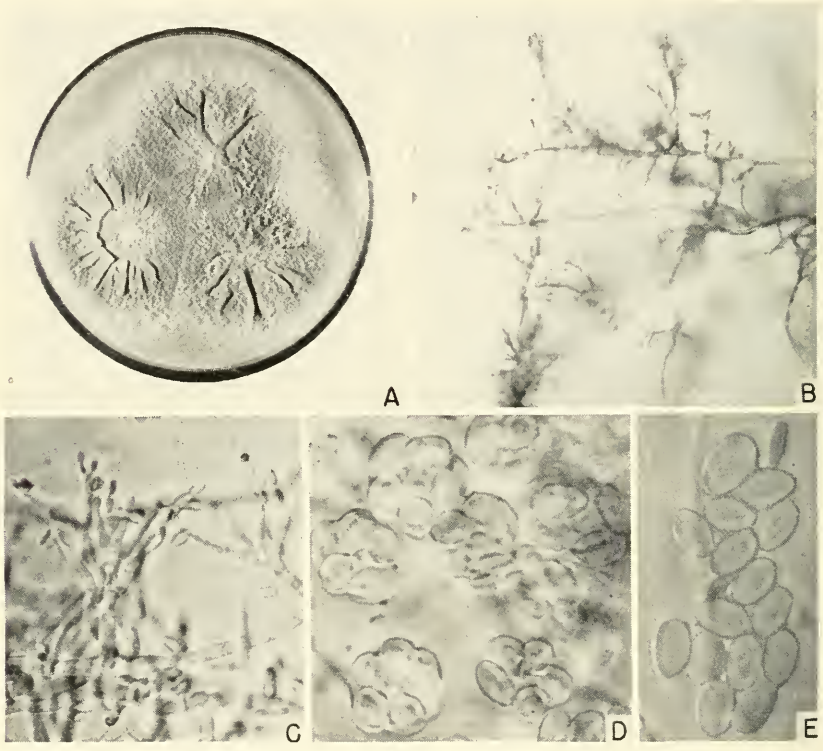


FIG. 171. *A–C*, *Paecilomyces varioti* Bainier, NRRL 1118. *A*, Ten-day-old colonies on Czapek agar. *B*, Colony margin showing characteristic ropiness and scattered and irregular fruiting structures, × 90. *C*, Detail of a small conidial structure showing the characteristic pattern of the sterigmata in this genus, × 600. *D* and *E*, *Byssochlamys fulva* Olliver and Smith, NRRL 1125, asci and mature ascospores, respectively; a conidium appears at upper right of latter figure.

spreading, almost white, deeply floccose, lightly sporing colonies on all substrata.

Sakaguchi, Inoue and Tada (1939) described as a new species, *Penicillium viniferum*, which represents a *Paecilomyces* that is like *P. varioti* in color but produces penicillate conidial structures of fairly regular pattern and sterigmata with prominent but shorter conidial tubes than typical *P. varioti* strains. A second culture also described as new by the same authors,

under the name *Monilia formosa*, represents a strain of *Paecilomyces* approximating *P. varioti*.

In nature, *Paecilomyces* represents an extremely common and variable group of molds. Comparative study of all available members of the group will be required to develop a sound nomenclature and to establish with certainty its natural relationships to *Penicillium* and other genera of saprophytic molds with which it is now oftentimes confused.

Paecilomyces varioti Bainier, in Bul. Soc. Mycol. France **23:** 26–27, Pl. VIII. 1907.

Synonym: *Penicillium divaricatum* Thom, in U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, pp. 72–73, fig. 29. 1910.
Spicaria divaricata (Thom) Gilman and Abbott, in Iowa State Col. Jour. Sci. **1:** 301. 1927.

Colonies spreading broadly upon all common media (fig. 171A), in shades of yellowish brown (avellaneous), *never green*, with superficial growth consisting mostly of trailing fertile hyphae or ropes of hyphae (fig. 171B), becoming powdery in appearance when mature; reverse of colony not discolored in some strains, developing bluish green shades in others; fertile hyphae septate, usually short, mostly creeping; conidial fructifications either terminal or on short branches (fig. 171C) of creeping or partially erect hyphae, consisting of separate sterigmatic cells, or of verticils, or series of verticils of branchlets and sterigmata irregularly distributed along the fertile hyphae; sterigmata 15 to 20μ by 3μ with long acuminate tubes usually bent away from the axis of the cell and widely divergent at the apices (fig. 11D), bearing long chains of conidia; conidia elliptical or fusiform, 5 to 7μ by 2.5 to 3.0μ, yellowish to brownish, smooth-walled, swelling in germination to 10μ and producing 2 or more tubes. The species is unmistakable when once seen in culture.

Thom's type of *Penicillium divaricatum*, upon which the above description was based, was first found in an empty mucilage bottle, Storrs, Connecticut, 1904. An enormous number of cultures with the basic characters of *Paecilomyces varioti* have been seen. These vary in the shade of color of colony and substratum, in floccosity, in the abundance and distribution of the so-called macrospores, in the arrangement of the sterigmata, and in the size of the conidia. Our Collection and records show organisms of this type from Japan, Manchuria, Europe, China, South Africa, South America, the Southwest Pacific, Australia, and from many parts of the United States. They have been observed among the molds from all soils examined. Representative strains include NRRL 1115 (Thom's No. 34 and the type of *Penicillium divaricatum*); NRRL 1118 from Fawcett in California in 1934;

NRRL 1124, from Simonart in 1936 as *Paecilomyces varioti* Bainier; and two strains received from the Centraalbureau under this name in July 1946.

Viewed in conjunction with the descriptions and figures found in the literature, the structural type here recognized as *Paecilomyces* is seen to be cosmopolitan and is found described under several generic names, including: *Corollium*, *Spicaria*, *Penicilium*, *Paecilomyces*, *Eidamia*, *Byssochlamys*, and perhaps others. No one at present knows this group well enough to establish sound lines of relationship among them.

Byssochlamys fulva Olliver and Smith, in Jour. Bot. **72:** 196–197; Pl. 602, figs. 1 and 2. 1933.

Authors' diagnosis as follows:

"Colonies growing well on most solid media, better on natural than on purely synthetic media, most readily at temperatures between 30° and 37°C.; on liquid synthetic media growing fairly slowly at 20°–25°, better at 30°; at 37° the spores are readily wetted by liquid media, and growth is very slow until the submerged mycelium reaches the surface: surface white, then buff to pale brown in central areas, slightly floccose or funiculose, after seven to ten days showing clusters of asci visible to the naked eye as minute globose masses partially embedded in the mycelial felt; reverse slowly turning pale brown; conidial fructification of the *Paecilomyces* type, conidiophores very variable in length, arising as side-branches from long trailing hyphae, simple or variously branched, 2–3μ in diameter, bearing whorls of sterigmata or solitary sterigmata at various points along the length, sessile or on short side branches; sterigmata short tubular or much swollen at the base and terminating in long slender tubes, frequently curved or bent away from the main axis, up to 25μ long and usually 2–3μ in diameter, but occasionally up to 7μ; conidia one-celled, hyaline, ovate to elongate, very variable in size but mostly 4–9μ x 2.3–2.5μ, borne in very long, unbranched, tangled chains; asci abundant on all media, produced in roughly globose clusters without any trace of peridium or enveloping hyphae, globose, 8-spored, 11–12μ in diameter; ascospores smooth, hyaline, ovate, 6–6.5μ x 4.3–4.5μ.

"The natural habitat has not yet been discovered, all isolations having been made from canned and bottled fruits. The mature spores can survive cooking for thirty minutes at 87°–88°C., which explains their survival in the processed cans and bottles, since the maximum temperature of sterilization, although it may exceed 90°, is maintained for only a few minutes."

The present species has been under observation in our Laboratory since 1933 without losing its capacity to produce abundant ascospores (fig. 171D and E). It is maintained as NRRL 1125.

The above description is drawn with sufficient care to obviate the necessity of any additional notes on our part, either cultural or morphological.

OCCURRENCE AND SIGNIFICANCE

Members of the genus *Paecilomyces* have been found in the most diverse environments in nature. Turesson (1916) isolated a strain from human

feces. Segal (1923) reported one as isolated from a guinea pig inoculated with the virus of typhus fever. We have had cultures from licorice root, from a hen's egg, from nut margarine, from soy products in China, from bread in Arabia, and from a quinine solution. Great masses of mycelium of this species were found deep in a pile of cabbage waste at a sauerkraut factory in Ohio where the temperature had reached 55°C. They have occurred frequently upon exposed military equipment, but their significance in process of deterioration has not been thoroughly explored.

Kita and Wai found their organism (proposed as a new species but undescribed) upon rotting boards in a cellar. Several strains were received from the Forest Products Laboratory in Madison, Wisconsin, as isolates from wood in various stages of discoloration or decay. *Penicillium divaricatum* has been reported as the cause of "yellow stain" in hardwood timbers in Australia. Robertson (1939), in London, reported the same species to grow well at 44°C. and to cause a yellow stain of oak timber during the kiln-drying process. Growth of the mold could be controlled by dipping the freshly sawed planks in an antiseptic bath containing one of the chlorinated phenols or by spraying the timber with a formaldehyde solution. Davidson, *et al.* (1942) isolated *Paecilomyces varioti* from brownish streaks in the heartwood of living oaks.

Shaposhnikov and Manteifel (1923) reported the production of citric acid (at 40°C.) by a thermophilic mold described as a new species, *Penicillium arenarium*. Thom (1930, pp. 546–547) regarded this as probably representing some member of the *Paecilomyces varioti* series. The culture has not been seen by us.

Sakaguchi, Inoue, and Tada (1939) reported two new species of molds, *Penicillium viniferum* and *Monilia formosa* to produce ethylene-α-β-dicarboxylic acid as their chief metabolic product. Types of the two species were secured from Sakaguchi and both were found to represent *Paecilomyces*.

An occasional strain appears to be parasitic. *Penicillium burei* was first isolated from an experimentally produced nodule and described as a new species in 1927 by Pollacci. Pirrone (1929) produced mycotic nodules in experimental animals but found the species to be less active than either *Sterigmatocystis nigra* (*Aspergillus niger*) or *Actinomyces bovis*. Thom (1930, p. 548) regarded Pollacci's species as a *Paecilomyces*, hence changed the name to *Paecilomyces burei* (Poll.) Thom.

Olliver and Rendle (1934) found *Byssochlamys fulva* to be an important factor in the spoilage of canned fruit in England. Typically the mold disintegrates the fruit tissue by attacking the pectinous substances. The species is unusually resistant. The ascospores will withstand a temperature of 86–88°C. for 30 minutes, hence are viable at the end of many canning

processes. It can grow under reduced oxygen tension and can tolerate SO_2 in plum syrups in concentrations up to 50 p.p.m., and in concentrations of 450 p.p.m. in a solution containing 10 per cent sucrose and 1 per cent peptone. *Byssochlamys fulva* grows over a pH range from 2.0 to 7.0, with optimum about pH 3.0. It will grow in nutrient media containing 6.0 per cent of either citric, tartaric, or malic acid. Old cultures have withstood immersion in 100 per cent alcohol for 30 weeks without loss of viability. The species has been isolated from field samples of strawberries, gooseberries, and several varieties of plums. Orchard soil is presumed to furnish a reservoir of infection.

Raistrick and Smith (1933) investigated the metabolic products of *Byssochlamys fulva* when grown upon Czapek-Dox solution containing 5 per cent glucose as a source of carbon. Mannitol was the chief metabolic product, yields equivalent to 30 per cent of the sugar consumed being obtained in about 2 months time. A new mold product, byssochlamic acid, $C_{18}H_{20}O_6$, M.P. 163.5°C, was also isolated from the metabolism solutions in yields of about 0.5 per cent. The substance is quite toxic to mice. The acid titrates as a tetrabasic acid, and has the same empirical formula as that attributed to glauconic acid II, another mold product reported by Wijkman (1931). It differs markedly from the latter, however, in certain other respects; glauconic acid II melts at 186°C.

Scopulariopsis

Scopulariopsis Bainier represents a third genus of molds which may not be closely related to *Penicillium* genetically, but which is characterized by conidial structures that are often more or less penicillate. Furthermore, these forms are unusually abundant in nature, especially upon vegetation in the latter stages of decay and upon aging or moldy products of animal origin that are relatively rich in protein. They occur regularly under conditions where many Penicillia abound, and bearing considerable resemblance to such forms, they have been commonly mistaken for species of *Penicillium* and have been so described.

The genus was characterized in essentially the following manner by Thom (1930, p. 511):

Scopulariopsis Bainier, in Bul. Soc. Myc. France **23:** 99–103; Pl. XI, figs. 1–6. 1907. Type species: *Penicillium brevicaule* Saccardo, t.893, in Fungi Italici.

Synonyms: *Acaulium* Sopp in Monograph, pp. 42–46. 1912.
Penicillium, sub-section VI, *Anomala*, in Biourge's Monograph, La Cellule **33:** fasc. 1, pp. 214–216. 1923.

Colonies *never green*, with aerial hyphae at least partly in trailing and anastomosing ropes (funiculose); conidiophores mostly short or even want-

ing, commonly borne along the funiculose hyphae; conidial apparatus variable, Penicillium-like, or consisting of varying and irregular aggregations of branches and sterigmata, at times reduced to single sterigmata scattered along the aerial hyphae; sterigmata more or less specialized, sometimes tapering gradually from a basal tubular section, or even the base itself, toward a conidium bearing apex, or narrowly tubular without tapering, cutting off conidia from the apex by cross walls; conidia more or less pointed or rounded at the apex and truncate at the base, with a more or less thickened basal ring surrounding a basal germinal pore, with walls usually thickened, and often variously marked or roughened; often colored but never in true greens.

Members of the genus commonly appear as agents of decomposition after the usual green Penicillia have ceased to be active; that is in the later stages of decay processes. They are generally more active in the decomposition of complex nitrogenous foods than are the Penicillia.

Bainier (1907) was probably right in separating from *Penicillium* the group of strains and species centering upon Saccardo's *Penicillium brevicaule*, the general structure of which was well known but the type of which had not been cultivated by Saccardo. Bainier isolated a series of forms showing considerable divergence in conidia and colony characteristics and described them as different species.

In describing *Acaulium* to include the same group of molds, Sopp (1912) observed the presence of dark-walled perithecia showing small but definite ostioles. He further observed that they produced an arsenical odor; that they decomposed milk, cellulose, resinous wood, paper and sawdust; that they grew poorly on pure cotton; and that they grew at higher temperatures than most Penicillia.

Biourge (1923) found in this type of organism the probable identification of Corda's *Penicillium anomalum*, hence called this lot of forms a subsection, *Anomala*, in the genus *Penicillium*.

Loubière (1924) described *Scopulariopsis candida* as the conidial stage of *Nephrospora mangini* new genus and species, with perithecia in general agreeing with the description of Sopp's *Acaulium albo-nigrescens*, which may well have been the same as Loubière's species.

Prior to Bainier's work (1907), members of the genus *Scopulariopsis*, as it is now generally understood, had been assigned to several different genera of Hyphomycetes by earlier mycologists. Harz (1871) put them in *Spicaria*. Oudemans (1902) put them in *Monilia*. Older workers, including Fresenius (1850–1863), Bonorden (1851), and Rivolta (1873) discussed them as *Torula* or *Oidium*. No one who has studied many strains of this group in comparison with the usual types of *Penicillium* believes them to be closely related to that genus.

Gosio (1892, 1896), Maasen (1902), Ceni (1907), Huss (1914), and other

workers in various lands have investigated these organisms, regularly identified as *Penicillium brevicaule,* on account of their biochemical usefulness in indicating the presence of minute traces of arsenic in the substratum through the evolution of arsenical gases from the growing culture. More recently, the whole problem of the evolution of "arsine" gases by these molds has been carefully studied by Professor Challenger and co-workers at the University of Leeds, England (see Topical Bibliography, p. 720).

Many strains of *Scopulariopsis* tend to develop while submerged in liquid, or below the surface of any substratum used. Such growth is usually accompanied by distortions, swellings, and vesiculation of the mycelial cells. Aerial fruiting structures may develop very slowly, partly on ropes of hyphae, partly on simple hyphae with considerable sterile areas. Sopp (1912) noted the extreme difficulty of the group, to which Biourge (1923) agreed, and added further that he was not satisfied with the disposition that he had made. Thom, in 1930, included the published descriptions which had appeared up to that time, but he despaired of establishing any orderly natural relationship of species and in the end listed them alphabetically.

Study of natural substrata shows species of *Scopulariopsis* to be abundant in every region surveyed. Miss Dale found them in English soil; Sopp isolated them in Norway; Saccardo, Gosio, Ceni, and others have reported them in Italy; Pribram's collection coming from Vienna was full of them as replacements of other organisms; others from Asia, South Africa, Brazil and Argentina, and hundreds of strains from different parts of the United States have been seen. We have isolated them from many sources including soil, stored grain, decaying vegetation, silk, leather, awnings and other exposed fabrics, and many varieties of old cheese both imported and domestic. They are especially abundant in old and over-ripe Camembert; and in the rooms where these cheese are ripened, species of *Scopulariopsis* are frequently so abundant as to produce a characteristic ammoniacal odor. They are fairly common upon stored meat. In one lot of musty hams, mycelium was found to be present deep in the tissues although mustiness was the only discernible effect of their activity.

Species of *Scopulariopsis* have been frequently reported to be parasitic to man and other animals. They represent a common cause of onychomycosis in which the nails become swollen, whitish, and brittle. They are responsible for some dermatomycoses, so-called "American blastomycosis," and may cause infections of the tongue and oral cavity. They are not an uncommon cause of mycoses of the feet. Many new species have been described either largely or wholly upon the bases of proven or suspected pathogenicity, generally without adequate regard for species already in the literature.

A considerable number of new species have been described by Zach (1934), van Beyma (1935, 1937, 1939), von Szilvinyi (1941), and others since the publication of Thom's Monograph in 1930. It is estimated that upward of 100 names for species of *Scopulariopsis* appear in the literature. No one has made a careful and thorough study of the group. Until someone can study in comparative culture upon various substrata all of the so-called species and varieties obtainable, the taxonomy and the relationships of species in the genus *Scopulariopsis* will remain in its present confused state.

In the meantime, we believe that our wisest course is to present a fairly general description covering the forms most commonly encountered which are, at the same time, representative of the type species *Scopulariopsis brevicaulis* (Sacc.) Bainier. Following this presentation a few notations will be made relative to groups of strains which we believe to be recognizable. In some cases these may be correlated with certain described species and varieties. No attempt will be made to give a complete and critical coverage of the genus *Scopulariopsis*.

Scopulariopsis brevicaulis (Sacc.) Bainier, in Bul. Soc. Mycol. France **23:** 99–103, Pl. XI, figs. 1–6. 1907.

Synonyms: *Penicillium brevicaule* Saccardo, in Fung. Italici t.893 and Michelia II, p. 547.

Penicillium anomalum Corda, in Icones Fungorum II, p. 18; Tab. XI, fig. 75. 1838.

Acaulium anomalum Sopp, "ad interim," in Monograph, pp. 65–67; Taf. VIII, fig. 75. 1912.

Monilia koningii Oudemans, in Arch. Neerland. Sc. Exact. et. Nat. p. 23; Taf. XXI. 1902.

Colonies on Czapek's solution agar spreading rather broadly in most strains (fig. 172A), more or less restricted in others, comparatively thin, plane, or irregularly but not deeply furrowed, at first grayish white, then avellaneous, or yellowish brown even to light chocolate, with surface characterized by closely crowded, short conidiophores to produce powdery conidial areas overgrown by loosely trailing floccose hyphae and ropes of hyphae in most strains, deeper and less heavily sporing in others, with margin usually indeterminate and broadly spreading, azonate or broadly zonate from an uneven production of conidia. Conidiophores short, mostly 10–30μ, arising directly from the submerged hyphae, or irregularly borne as lateral and perpendicular branches from trailing aerial hyphae and ropes of hyphae (fig. 172B). Conidial fructifications either simple and unbranched, sparingly branched, or consisting of verticillate and irregular branching systems bearing numerous divergent chains of conidia (fig.

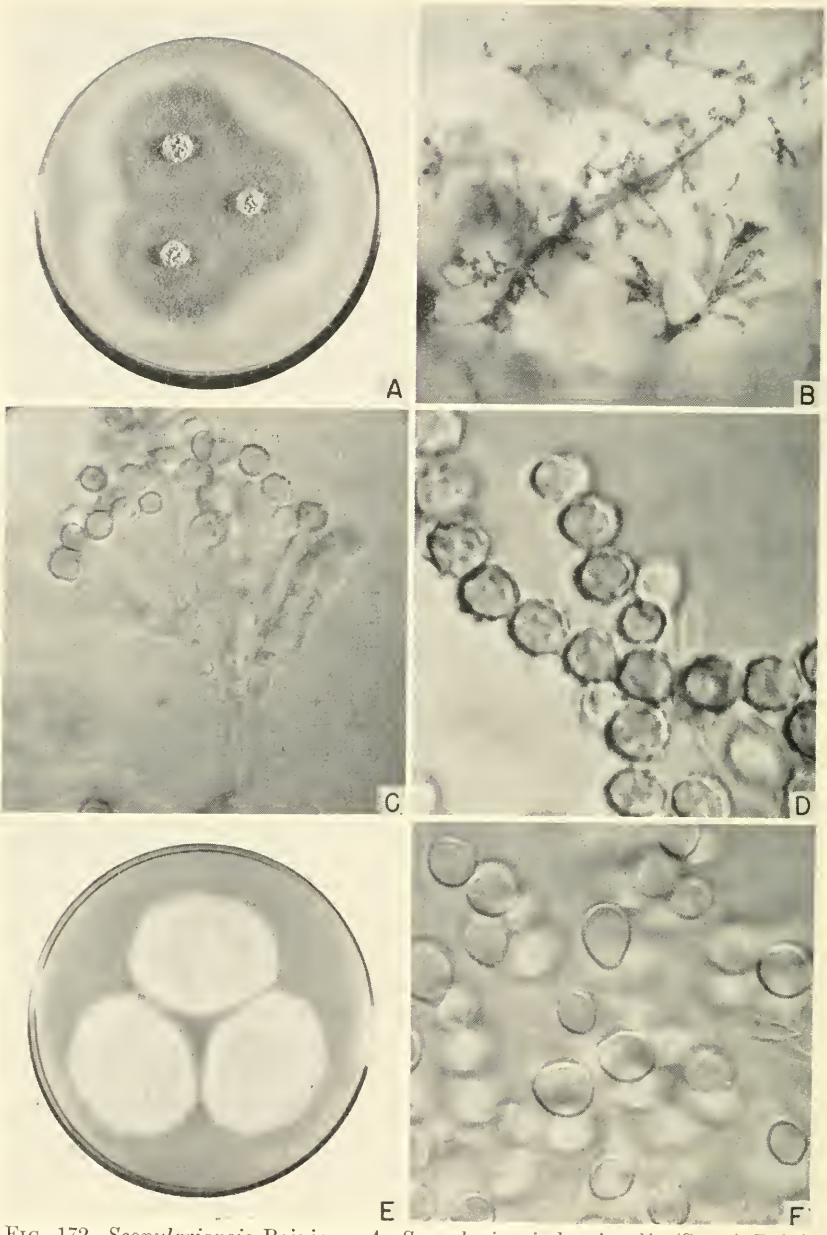


FIG. 172. *Scopulariopsis* Bainier. *A*, *Scopulariopsis brevicaulis* (Sacc.) Bainier, NRRL 1096, on Czapek agar at ten days. *B*, Marginal area of colony as seen under low power, × 105. *C*, Penicillate conidial structure, × 750. *D*, Mature conidia of same species showing roughened walls, × 1300. *E*, *S. brevicaulis* var. *glabra* Thom, NRRL 2157, on Czapek agar at ten days. *F*, Mature conidia of the same strain showing thick, smooth walls. The production of conidia with flattened, truncate bases is characteristic of the genus.

172C), often 150μ in length in old colonies. Sterigmatic cells often continuous with the conidiophores, variable, up to 20μ by about 3.0 to 4.0μ, sometimes tapering to slender conidium bearing tubes, in other cases essentially uniform in diameter throughout. Conidia somewhat pear-shaped, thick-walled, characteristically tuberculate (fig. 172D) but smooth when young and often appearing so in liquid mounts under oil immersion, commonly measuring 6.5 to 7.5μ by 7.5 to 9.0μ, avellaneous to light brown in mass, viable for several years, germinating by a single tube from the thin center of the broad base into a bulbous enlargement from which mycelial hyphae about 2μ in diameter arise.

Colonies on steep agar usually growing more rapidly, tending to be looser in texture, and often sporulating somewhat more abundantly than upon Czapek agar. Their general appearance and color is, however, essentially the same. Conidial structures duplicate those seen on Czapek.

Colonies on malt agar are usually thin, and often very restricted in growth. Sporulation varies from abundant to almost lacking, depending upon the strain.

Colonies digest milk and liquefy gelatin with a strong ammoniacal odor. They grow very rapidly upon neutral or alkaline media, but more slowly or hardly at all in acid media, hence their appearance on malt agar.

Members of the genus *Scopulariopsis* vary greatly in the shade of yellow-brown produced in conidial areas, including occasional forms which are white or nearly so. None produce true green spores, although certain forms have been assigned to the genus which produce conidia with walls pale greenish black. Conidia may be smooth or rough, and vary greatly in shape, size, and intensity of color. The appearance of a truncate base appears to be consistent and characteristic of all forms. No one has yet reported a comparative study of the group from which valid lines of separation among species could be established.

Thom, in 1910, recognized two varieties of *Scopulariopsis brevicaulis* (Sacc.) Bainier (as *P. brevicaule* Sacc.) based upon the character and color of the conidia produced in strains under examination. *Penicillium brevicaule* var. *album* was established to include occasional strains encountered in cheese investigations which had rough but colorless conidia. The variety did not otherwise differ from the species. *Penicillium brevicaule* var. *glabrum* was established to include strains with smooth-walled colorless conidia. Culturally, this variety likewise duplicated the species except for an absence of avellaneous color (fig. 172E) and the production of smooth-walled conidia (fig. 172F).

In his Monograph, Thom (1930) included but did not attempt to classify descriptions of species reported up to that time. Since that date many additional species have been described.

We have made a limited examination of all strains available from our Collection, and also of many strains representing "species" received from the Centraalbureau in 1946. We hesitate to attempt any separation of species until the whole group can be thoroughly restudied. Nevertheless, with the view that our observations may be of some value to the user of this Manual, we are listing below certain patterns of growth and morphology represented by the strains in our possession. Named cultures are cited as they are represented in the different groupings.

Group I: Represented by the species *Scopulariopsis brevicaulis* (Sacc.) Bain. in its typical aspect as described above. Contained herein are numerous strains maintained in our Collection and two received from Baarn under this name. Cultures in our possession, designated *S. brevicaulis* var. *hominis* Brumpt and Langeron (in Brumpt, 1913) differ from the species, if at all, only in producing conidia of slightly darker color with walls generally more conspicuously roughened.

Group II: Colonies differing from the above in showing increased ropiness and lighter colors in white to light beige shades, and conidia irregularly roughened with many cells appearing smooth. Growth on malt agar is very slow or lacking. Represented by two strains received from Baarn as *Scopulariopsis brevicaulis* var. *alba* Thom, and two strains received as *S. insectivora* (Olsen-Sopp) Biourge. A third strain received under the latter name represents a typical strain of *S. brevicaulis*.

Group III: Colonies similar to Group I in general texture and pattern and consistently light colored as in Group II, but showing conidia consistently smooth-walled. Growth on malt agar is restricted, usually nonsporulating. Represented by cultures in our Collection, and by strains received from Baarn as *Scopulariopsis brevicaulis* var. *glabra* Thom, and others from Baarn as *S. candelabrum* Loub., *S. brumptii* Salvanet-Duval, and *S. bestae* (Poll.) Nann.

Group IV: Colonies like the preceding in texture and appearance, with conidia similarly smooth-walled; producing cellular bodies ranging from white to blackish which we presume to be abortive perithecia (no ascospores have been seen). Represented by two strains from Baarn as *S. alboflavescens* Zach. This species was described originally as ascosporic, with small black perithecia.

Group V: Colonies conspicuously furrowed, dark dull brown in color; conidia heavy-walled but consistently smooth. Colonies growing very restrictedly on malt agar. Represented by strains received from Baarn as *Scopulariopsis arnoldi* Mang. and Pat., and *S. fusca* Zach.

Group VI: Colonies deeper, with margins tending to be abrupt; conidial areas in dull grayish to deep brown shades, conidia smooth with walls thick and greenish brown in color. Growth on malt agar is restricted.

Represented by strains from Baarn as *Scopulariopsis atra* Zach, *S. croci* v. Beyma, *S. danica* v. Beyma, and *S. sphaerospora* Zach.

Group VII: Colonies growing restrictedly and very thinly on Czapek, heavy sporing but equally restricted on steep agar, spreading on malt with conidial areas in dark olive green to fuscous shades; conidia globose or nearly so, with walls coarsely roughened. Represented by a strain in our Collection tentatively identified as possibly representing a form similar to Sopp's *Acaulium nigrum.*

Group VIII: Colonies spreading broadly on all media, very thin on Czapek, heavily sporing on steep and malt agars. Conidial areas in deep slate colors. Conidia elliptical and with basal ends less conspicuously flattened than in any of the above, forming long chains and the chains remaining adherent in fluid mounts, walls smooth, appearing dematiaceous. Represented by a strain in our Collection tentatively identified as possibly approximating *Scopulariopsis costantini* (Bainier) Dale. The pattern of the penicillus in this strain is somewhat suggestive of the polyverticillate Penicilli (Chapter XIV).

Group IX: Colonies somewhat restricted, wet, tending to be strongly funiculose, essentially non-sporulating on Czapek and steep agars; on malt agar sporulating moderately well, in yellow-gray shades, producing conidia of two types, (1) elliptical, smooth conidia in fairly long aerial chains, and (2) globose, conspicuously roughened conidia in shorter chains adjacent to the substratum. Represented by a culture received from Baarn as *Scopulariopsis diversispora* v. Beyma.

Ascosporic Phase

Curzi (1930, 1931), Emmons and Dodge (1931), and Jones (1936) have described ascosporic stages belonging to the genus *Microascus* Zukal (1890) for molds with a *Scopulariopsis* conidial phase. Loubière (1924) had described a new genus and species, *Nephrospora mangini*, for the ascosporic stage of *Scopulariopsis candida* (Pers.) Loub. Both Curzi, and Emmons and Dodge regarded *Nephrospora* as synonymous with the older genus *Microascus*, as they did also Sopp's *Acaulium albo-nigrescens* (1912) which was described with small black globose to pear-shaped perithecia with distinct ostioles. Zach (1934) described *S. albo-flavescens* as ascosporic with small black perithecia.

The ascocarps or perithecia of *Microascus* species are characterized by heavy black walls and are ostiolate. They are thus clearly different from any of the ascosporic structures seen in any section of the genus *Penicillium.* Upon the basis of these structures, Curzi would transfer the genus *Microascus* to the Sphaeriales. Emmons and Dodge regard the genus as making more complete a series of genera that is transitional from *Aspergillus* and

Penicillium through *Thielavia* and *Microascus* to *Chaetomium*. The ascosporic phase of these fungi, no less than the conidial stage, is deserving of more careful study.

Occurrence and Significance

Members of the genus *Scopulariopsis*, and particularly *S. brevicaulis* (Sacc.) Bainier, are unusually abundant in nature. They are isolated regularly from soil. They are fairly tolerant of drought and commonly appear upon materials such as stored grain, forage products, and all types of semi-dry vegetation undergoing slow decay. They often develop upon organic residues after the readily available nutrients are exhausted, and after most other micro-organisms have completed their roles in the decomposition process. They thrive on substrata that are relatively rich in nitrogen and are commonly isolated from products of animal origin including leather, wool, bone, cured meats, and ripening cheese. Members of the genus are sometimes isolated from insects (Sartory, *et al.*, 1930). Strains are not infrequently isolated from skin and nail infections, and less commonly from other parts of the body. Many species have been described as parasitic or semi-parasitic.

Biochemically, the group is of considerable interest because of the capacity of most strains to attack arsenic compounds with the evolution of arsenical gases characterized by a garlic odor. Occasional cases of arsenic poisoning of individuals living in houses with walls painted or papered with arsenic containing pigments, such as Scheele's green, were first reported more than a century ago. Such deaths were at first attributed to the inhalation of pigment particles as dust. Later some investigators suggested that the molds growing upon the walls might play an active role. Gosio, in the 1890's, was the first to make a systematic study of the whole question. He found *Penicillium brevicaule* Sacc. to be quite active, and developed a method for detecting minute traces of arsenic in different materials, the mold producing a more or less intense garlic odor in the presence of arsenic. Gosio's work was continued by his associate Biginelli (1900) who concluded that the volatile gas was diethylarsine. Meanwhile Maasen (1902), Huss (1914), and others reviewed the matter of arsenic evolution and its possible relation to pathological symptoms.

The whole question of mold induced arsenic poisoning was brought to a sharp focus by the so-called "Forest of Dean Case" in 1932, wherein the death of two children in Wales was suspected of being due to arsenic poisoning (see Lerrigo, 1932). Analysis of body tissues showed the presence of arsenic, and exposure of filter paper saturated with silver nitrate to the air of the room gave a positive test for arsenic. An investigation of the subject of gaseous arsenic evolution by molds was initiated at the University

of Leeds by Professor Frederick Challenger and associates at this time, and in May 1932 the gas was identified as trimethylarsine, $(CH_3)_3As$. An intensive study of the whole problem has since been conducted and a long series of papers have been published in British Chemical journals (see Topical Bibliography, p. 720). The evolution of volatile gases of tellurium and selenium was likewise investigated. In 1945 Challenger published in *Chemical Reviews* an important paper entitled "Biological Methylation" in which 219 references are cited. Without doubt this constitutes the best available summary of information on the subject. In the same year, Bach published in *Biological Reviews* a paper under this same title but more limited in scope.

Thom and Raper (1932) reported other species of molds to produce arsenical gases, but found none of these to be as active as *Scopulariopsis brevicaulis*.

A number of investigators have followed Gosio in proposing the use of *Scopulariopsis brevicaulis* for detecting small amounts of arsenic in foods and other products. Teichert (1934) used it to detect the presence of arsenic in metal foils used as cheese wrappings. Breiter (1936) used it as a qualitative test but questioned its usefulness in quantitative work. Smith and Cameron (1933), on the other hand, outlined a method by which amounts as low as 1 p.p.m. could be detected in food samples. Gosio republished on this subject as recently as 1932.

Burgess (1928, 1930, 1931) reported *Penicillium brevicaule* to be one of the molds most commonly encountered in his investigations of the microbiology of wool. Davis (1933) found *P. brevicaule* to be common on mildewed areas of silk and cellulose acetate cloths.

Nakazawa and Takeda (1928), studying the foods produced by natives in Java and Sumatra, reported *Penicillium brevicaule* to be the principal mold concerned with the preparation of "Ontjom" from ground nuts, and "Tempeh" from soybeans.

Christensen and Moses (1945) reported *Scopulariopsis brevicaulis* to be capable of rapid delamination of yellow birch plywood when either casein or soybean glue was used. Incorporation of 5 per cent sodium trichlorophenate in the glue prevented any weakening of the glued joints in accelerated tests running for 26 days.

Some strains of *Scopulariopsis brevicaulis* produce a substantial amount of proteolytic enzymes. Ayres and Niedercorn, in 1942, obtained a patent covering the use of such cultures.

Pathogenicity

Scopulariopsis represents a fairly common cause of onychomycosis, with nails commonly becoming brittle, thickened, and white. Cases have been

reported by Brumpt (1910), Emile-Weil and Gaudin (1919), Sartory and Sartory (1925), Sartory, *et al.* (1930), Artom (1936), Nicolas, *et al.* (1936), and others. The species usually reported is *Scopulariopsis brevicaulis.*

Strains of *Scopulariopsis* are likewise commonly responsible for dermatomycoses of the feet and other parts of the body. Such have been reported by Sartory (1916), Raymond and Parisot (1916), Leger and Nogue (1922), Castellani (1925), Weisz (1934), Olah (1935), Clarrocchi (1935), and others. Again the species usually reported is *Scopulariopsis brevicaulis.*

Kawatsure (1933) and Bertaccini (1934) have reported strains of *Scopulariopsis* as causative agents in so-called "American blastomycoses," the responsible species being reported as *Scopulariopsis americana* and *S. bertaccini*, respectively. Markley, *et al.* (1936) isolated *S. brevicaulis* from an ulcerating granuloma involving the inguinal and perineal regions of a young woman. Greco (1916) had reported *S. venerei* n. sp. to be responsible for cases of venereal granuloma.

Panayotatou (1927) isolated a mold from the tongue of an Egyptian boy which he named *Penicillium linguae*, but noted that it belonged to the genus *Scopulariopsis.* Neto and Martins (1931) subsequently isolated a mold from a similar case in Portugal, and described the pathogen as a new species, *S. lingualis.*

No attempt is made to present a complete coverage of *Scopulariopsis* in relation to diseases in man and animals. It should be noted in passing, however, that members of this genus are commonly reported, and that much of the animal pathology attributed to species of *Penicillium* is in reality due to different forms of *Scopulariopsis* which have erroneously been referred to the genus *Penicillium.* For more detailed information regarding *Scopulariopsis* in relation to medical mycology, the reader is referred to texts on this subject by Dodge (1935), Conant, *et al.* (1945), and others.

PART III

REFERENCE MATERIAL

Chapter XVI

TOPICAL BIBLIOGRAPHY

In preparing this Manual the writers have attempted to discuss, in connection with the different series of Penicillia, the principal physiological and biochemical characteristics of individual species, or groups of species, in so far as these are known. It has not been possible, however, to summarize in any one place the information available regarding particular subjects, e.g., the formation of organic acids, the production of antibiotics, the elaboration of pigments and coloring substances, etc. Believing that titles of papers dealing with these and other general topics will prove valuable to the user of the Manual as he seeks to ferret out information regarding selected subjects, we have compiled a topical bibliography covering the principal activities and applications of the Penicillia as these relate to agricultural, industrial, or academic problems and pursuits. In many cases we have included here references which do not appear in the text or in the General Bibliography. Even so, we have not attempted to present a complete bibliography, which on a single subject such as penicillin would probably run to two thousand or more titles. We have, however, endeavored to present a sufficient number of references to provide the investigator with a guide to the literature of various fields. Every effort has been made to select the most important papers for citation. A list of topics under which references are presented follows.

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Chapter XVII

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PART III.

REFERENCE MATERIAL

Chapter XVIII

CHECK LIST OF SPECIES AND GENERA

GENERIC NAMES FOUND APPLIED TO PENICILLIA

Page

Acaulium Sopp, in Monogr., Videnskap. Sk. I. Mat.-Naturv. Kl. no. 11, p. 42. 1912. Type species *Penicillium brevicaule* Saccardo 16

Syn. *Scopulariopsis* Bainier 24

Aspergilloides Dierckx, in Soc. Scien. Brux. **25:** 83–89. 1901. Name used to include species now assigned to the Monoverticillata section of *Penicillium* 17

Aspergillopsis Sopp, in Monogr., pp. 201–202, Taf. XX, fig. 149 and Taf. XXIII. 1912. Sopp proposed to use this name for some forms intermediate between *Aspergillus* and *Penicillium* but it has not been accepted by critical workers 17

Byssochlamys Westling, in Svensk Bot. Tids. **3:** 134, Taf. 4. 1909. This genus was established to cover an ascosporic form with a *Paecilomyces*-like conidial phase 17

Carpenteles Langeron, in Compt. Rend. Soc. Biol. Paris **87:** 343–345. 1922. A new genus established to include ascosporic Penicillia with perithecia at first sclerotioid. *P. glaucum*, as discussed by Brefeld, was cited as type 17

Citromyces Wehmer, in Beitr. z. Kennt. einh. Pilze I, pp. 1–92, Tafel I and II. Hannover and Leipzig, 1893. The genus was established to include certain citric acid producing molds with morphology which indisputably places them in the Monoverticillata section of *Penicillium* 18

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Clonostachys Corda, in Prachtflora, p. 31, Taf. XV. 1839. Type species *C. araucaria* Corda. A genus characterized by penicillate conidial structures bearing conidia in chains typically at an angle to the axis of the fruiting mass; closely related to, if not synonymous with, *Gliocladium* . 18

Coremium Link, in Obs., p. 19. 1809. Link's genus was created to include forms with penicillate conidial structures compacted together to form upright stalks or coremia 19

Corollium Sopp, in Monogr., pp. 98–99. 1912. See also Olav Johan-Olsen (Sopp) in Pharmacia, no. 22 and 23. 1904.

Syn. *Paecilomyces* Bainier 19

Dactylomyces Sopp, in Monogr., pp. 33, 35–42, Taf. III, figs. 14–21 and Taf. IV, figs. 22–30. 1912. Type species: *D. thermophilus* Sopp 20

Syn. *Thermoascus* Miehe. A little studied genus of uncertain relationship, producing perithecia and ascospores suggestive of the *P. lutem* series and large rebranched conidial structures ... 20

Eidamia in Horne and Williamson (Ann. Bot **37:** 393–432, figs. 1–13. 1923). Represented a *Paecilomyces*. Not *Eidamia* Lindau, in Rabenhorst, Kryptogamen-Flora, Pilze VIII: 123. 1904–1907 20

Eupenicillium Ludwig, in Lehrb. niederen Krypt. Stuttgart, 1892, pp. 263–265. A genus established to include ascosporic *P. glaucum* as discussed by Brefeld. It has not been accepted or used by any critical worker ... 20

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Gliocladium Corda, in Icones Fungorum **IV:** 30–31, Taf. VII, fig. 92. 1840. Type species: *G. penicilloides* Corda, *ibid.* Latin description repeated in Icones **V:** 14. 1842, with a brief paragraph in German. Characterized by penicillate fruiting structures with the conidia massed in balls of slime 20

Gymnoascus Baran., in Bot. Zeit. p. 158. 1872. Ascosporic forms with condial fruiting structures sometimes more or less penicillate 21

Isaria Persoon, in "Disp." pp. 41, 74. 1797. Certain coremiform Penicillia approximate the characters of *Isaria*; while some species of *Isaria* simulate strongly funiculose strains of *Penicillium* 21

Lysipenicillium Brefeld, in Unters. Gesammtgeb. der. Myk. **14:** 209–210. 1908; and **15:** Taf. VII, figs. 1–7. 1912. Type species: *L. insigne* regarded as probably representing a *Gliocladium* 22

Metarrhizium Sorokin, in Zeit. der Kaiserlichen Landwirtschaftlech Gesellschaft für Neurussland, Odessa 1879: 268 (*fide* Pope, 1944). Type species: *M. anisopliae* (Metsch.) Sorokin. Vuillemin and others have regarded as *Penicillium* forms which are generally assigned to *Metarrhizium* 22

Subgenus *Microaspergillus* Wehmer, in Monogr. 1901. Biourge used this to include a series of strains regarded by him as new and as bridging the gap between *Aspergillus* and *Penicillium* 23

Monilia Persoon, emend. Sacc. Mich. II, p. 17 nec Fr., in Sylloge **IV:** p. 31. 1886. This genus represented a very broad usage based upon conidia in unbranched chains; contained *Aspergillus*, *Penicillium*, and many other genera now recognized 23

Subgenus *Monoverticillium* Biourge, in Bul. Ass. Anc. El. Ec. Brass. Univ. Louvain, No. 3. 1920. Apparently used synonymously with Dierckx's *Aspergilloides* which represented monoverticillate Penicillia 23

Paecilomyces Bainier, in Bul. Soc. Mycol. France **23:** 26–27, Pl. VII. 1907. Type species: *P. varioti* Bain 23

Syn. *Penicillium divaricatum* Thom and *Eidamia catenulata* Horne and Williamson 24

Probable Syn.: *Corollium* Sopp and some species of *Spicaria* Harz 24

Scopulariopsis Bainier, in Bul. Soc. Mycol. France **23:** 98, pl. XI. 1907. Type species: *P. brevicaule* Saccardo 24

Syn. *Acaulium* Sopp 16

Spicaria Harz, in Bul. de la Soc. Imp. des Nat. de Moscou **44:** 51. 1871. Generally thought to include molds with verticillately branched and strongly divergent conidial structures. Tends to merge into *Penicillium* through *P. lilacinum* 24

Stysanus Corda is designated as a subgenus of *Penicillium* in Sopp's Monogr., pp. 78–79. 1912. Biourge (1923) proposed to consider *Stysanus* with *Penicillium* since penicillate conidial structures are sometimes seen.. 25

Synpenicillium Costantin, in Bul. Soc. Mycol. France **4:** 62–68, Pl. XIV, figs. 10–17. 1888. Type species: *Synpenicillium album* Cost 25

Syn: *P. costantini* Bainier, Bul. Soc. Myc. France **22:** Pl. 11, figs. 1–6. 1906. Regarded by Thom (1930) as representing a form of *Scopulariopsis* 25

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P. abnorme B. and Br., in Ann. and Mag. Nat. Hist. **7**, 5th series: 130, Pl. III, fig. 4. 1881. Thom, The Penicillia, p. 575. 1930. Not a *Penicillium*, if the figures are correct.

P. acidoferum Sopp, in Monogr., pp. 188–189; Taf. XXI, figs. 146; Taf. XXIII, fig. 34. 1912. Thom, The Penicillia, p. 361. 1930. Species not identifiable but suggests *P. canescens* Sopp as presented in this Manual.

Scop. acremonium (Delacroix) Vuillemin, in Bul. Soc. Mycol. France **27:** 148. 1911.

Syn: *Monilia acremonium* Delacroix, in Bul. Soc. Mycol. France **13:** 114, Pl. IX, fig. C. 1897. Identity of strains studied unknown.

P. aculeatum Raper and Fennell, in Mycologia **40:** 535–538, fig. 10. 1948..... 639

P. adametzi Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 507–509; Taf. 47, 61. 1927. Thom, The Penicillia, pp. 194–195. 1930..... 228

P. aeremonium (*Monilia*) Delacr. 1897. Misspelling for *acremonium* in Biourge's Liste Onomastique,* p. 100. 1923.

P. aerugineum Sopp, in Monogr., pp. 145–147, Taf. XVI, fig. 115; Taf. XXII, fig. 11. 1912; see Thom, The Penicillia, p. 552. 1930. Sopp cites green perithecia seen once! Conidia 4 to 5μ in diameter. No such organism is known to us.

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P. aeruginosum Demelius, in Verhandl. Zool.-Bot. Gesellsch. Wien **72:** 76–77, fig. 6. (1922) 1923. Thom, The Penicillia, p. 420. 1930. Probably represents a synonym of *P. urticae* Bainier.

P. aeruginosum Dierckx, in Soc. Scientifique Bruxelles **25:** 87. 1901. Thom, The Penicillia, pp. 414–415. 1930. Synonym of *P. italicum* Wehmer..... 529

Citromyces affinis Bainier and Sartory, in Bul. Soc. Mycol. France **28:** fasc. 1, pp. 39–43; Pl. I, figs. 1–7. 1912. Not identified. Figures indicate some ramigenous form..... 249

P. africanum Doebelt, in Ann. Mykol. **7:** 315–338. 1909. Thom, The Penicillia, pp. 465–466. 1930. Regarded as synonymous with *P. funiculosum* Thom..... 620

P. agaricinum (*Gliocl.*) Matruchot, 1893. In Biourge's Liste Onomastique, p. 100. 1923.

Scop. alba Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 172. 1941.

Citromyces albicans Sopp, in Monogr., pp. 128–129, Taf. XIV, fig. 101; Taf. XXII, fig. 10. 1912. Probably a member of the *P. frequentans* series..... 175

P. albicans Bainier, in Bul. Soc. France **25:** 18, Pl. V, figs. 8 and 9. 1907; Thom, The Penicillia, p. 495, fig. 87. 1930..... 669

P. albidum Sopp, in Monogr., pp. 186–187, Taf. XXI, fig. 144; Taf. XXIII, fig. 33. 1912. Thom, The Penicillia, p. 350. 1930..... 329

P. albo-cinerascens (*Oosp.*) Maublanc, 1903. In Biourge's Liste Onomastique, p. 100. 1923.

Scop. albo-flavescens Zach, in Österr. Bot. Zeitsch. **83:** 177–179, figs. 3 and 4. 1934..... 700

P. albo-marginatum Biourge, in

* Biourge included in his Mongraph (La Cellule **33:** fasc. 1, pp. 100–106. 1923) a *Liste Onomastique* in which he arbitrarily transferred to *Penicillium* a long list of species described as *Coremium*, *Acaulium*, *Isaria*, and other genera.

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Monogr., La Cellule **33:** fasc. 1, Col. Pl. XIII and Pl. XXII, fig. 129. 1923. Thom, The Penicillia, p. 575. 1930.

Syn. *Aspergillus albo-marginatum* Biourge; some member of the *A. restrictus* series.

Acaulium albo-nigrescens Sopp, in Monogr., pp. 70–76, Taf. VI and VII, figs. 40–63. 1912. Probably based upon some *Scopulariopsis* 695

Citromyces albo-roseum Sopp, in Monogr., pp. 122–125, Taf. XV, fig. 106; Taf. XXII, fig. 7. 1912. A monoverticillate form not identified since described. Perithecia reported but no asci seen. Possibly some form near *P. thomii* Maire.

P. albo-roseus (*Cit.*) Sopp. In Biourge's Liste Onomastique, p. 100. 1923.

Synpenicillium album Costantin, in Bul. Soc. Mycol. France **4:** 62–68, Pl. XIV, figs. 10–17. 1888.

Syn. *Scop. costantini* (Bain.) Dale, *q.v.*

P. album Epstein, in Archiv f. Hyg. Bd. 45, Hft. **4:** 360. 1902. Synonym of *P. camemberti* Thom.

P. album Preuss, in Linnaea **24:** 135. 1851. Thom, The Penicillia, p. 553. 1930. Preuss' material is not identifiable. For subsequent use of the name see *P. camemberti* Thom and *P. caseicolum* Bainier (p. 427).

P. album Rivolta, in Paras. Veget., p. 452, 1873. Thom, The Penicillia, p. 553. 1930. Not recognizable; may have been a white mutant of some green species.

P. album camemberti, name applied to culture listed as No. 601 in Catalogue of the Natl. Coll. of Type Cultures, Lister Institute, London, p. 26, 1922. Undoubtedly this is an incorrect form for *P. camemberti* Thom.

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Coremium alphitopus Secretan, in Myc. Suisse III, pp. 539–540. 1833. Thom, The Penicillia, p. 405. 1930. One of two varieties studied represents (A) *P. expansum* Link, the other (B) possibly *P. claviforme* Bainier .. 515

P. alquieri (*Oospora*) Delacr., 1897. In Biourge's Liste Onomastique, p. 100. 1923.

P. amethystinum Wehmer (nomen nudum) was cited by Biourge (Monograph, La Cellule **33:** fasc. 1, pp. 221–222, Col. Pl. VI, Pl. X, fig. 56. 1923) as a synonym of *P.* (*Scop.*) *rubellum* Bainier. Cultures received from Biourge under both names proved to be *P. lilacinum* Thom 288

P. amyli (*Stysanus*) Delacr., 1897. In Biourge's Liste Onomastique, p. 100. 1923.

P. anisopliae (Metschnikoff) Vuillemin, in Bul. Soc. Mycol. France **20:** 214–222, Pl. 11, figs. 1–8. 1904. Thom, The Penicillia, p. 434. 1930. Represents *Metarrhizium anisopliae* (Metschnikoff) Sorokin 22

P. anomalum Corda, in Icones Fung. II: p. 18, Tab. XI, fig. 75. 1838 697

Syn. *Spicaria anomala* Harz, cited Sacc. Syll. **4:** 167. 1886. Regarded by Thom, 1930, p. 517, as probably a *Scopulariopsis*.

Acaulium anomalum "ad interim" Sopp, in Monogr., pp. 65–67, Taf. VIII, fig. 75. 1912 697

Syn. *P. brevicaule* Saccardo.

P. aphodii (*Spicaria*) Vuillemin, 1910. In Biourge's Liste Onomastique, p. 100. 1923.

P. äquabile v. Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 161–162, fig. 16. 1941. Description and figures indicate a member of the Lanata not far from *P. aurantiocandidum* Biourge. No culture has been available.

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P. arachnophila (*Gibell.*) Vuillemin, 1911. In Biourge's Liste Onomastique, p. 100. 1923.

P. arbuscula (*Corem.*) H. Fischer, 1910. In Biourge's Liste Onomastique, p. 100. 1923.

P. arenarium Shaposhnikov and Manteifel, in Trans. Sci. Chem.-Pharmaceut. Inst., Moscow **5:** 1–64, figs. 1923. In Russian. Clearly some *Paecilomyces*..... 689

Scop. argentea Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 172, fig. 26. 1941.

P. armeniacum Berkeley, in Introduction to Cyptogamie Botany, p. 298, fig. 68c. 1857. Thom, The Penicillia, p. 576. 1930. Berkeley's figure shows branching chains of spores, hence it is not a *Penicillium*. It has been regarded as *Monilia sitophila* by some.

P. arnaudi Biourge (?). A culture under this name was brought by Dr. Simonart from the Biourge Collection in 1936. No description is known. The culture approximated *P. roqueforti* Thom.

Scop. arnoldi (Mangin and Pat.) Vuill., in Bul. Soc. Myeol. France **27:** 137–152. 1911..... 700

Syn. *Monilia arnoldi* Mangin and Patouillard.

P. aromaticum I (Roquefort) Sopp, in Monogr., pp. 155–156, Taf. XVII, figs. 118 and 119; Taf. XXII, figs. 7 and 8. 1912. Thom, The Penicillia, p. 280. 1930. Name applied to some member of the *P. roqueforti* series.

P. aromaticum ("Gammelost") Sopp, in Monogr., pp. 159–161, Taf. XVII, fig. 123; Taf. XXII, fig. 10. 1912; also referred to as *P. aromaticum II* by Sopp. Thom, The Penicillia, p. 286. 1930. Member of *P. roqueforti* series, and probably synonymous with that species..... 400

P. aromaticum III Sopp, in Centbl. f. Bakt. etc. (II) **4:** 161–169. 1898; cited in Sopp's Monogr., p. 179, 1912, without description but as synonym of *P. camembert* Sopp which is synonymous with *P. camemberti* Thom published earlier..... 426

P. aromaticum casei Johan-Olsen (Sopp), in Centbl. f. Bakt. etc. (II) **4:** 161–169. 1898; cited by Saccardo, Syll. **22:** 1278. 1913. Thom, The Penicillia, p. 280. 1930. Name applied to some member of the *P. roqueforti* series.

P. arsenici Gosio, in Boll. Inst. Sieroterap. Milan. **11:** 597–602. 1932. This usage was employed for a mold used to detect minute trace of arsenic in food products. Possibly referred to a *Scopulariopsis*.

P. aspergilliforme Bainier, in Bul. Soc. Myeol. France **23:** p. 14, Pl. IV, figs. 17–23. 1907. Apparently a monovertieillate form in the *P. frequentans* series. Not identified by subsequent workers.

P. aspergilliformis (*Gibell.*) (Rostrup) Vuillemin, 1911. In Biourge's Liste Onomastique, p. 100. 1923.

P. asperulum Bainier, in Bul. Soc. Myeol. France **23:** 17, Pl. IV, fig. 13–18. 1907. See also Westling, Arkiv f. Bot. **2:** 140. 1911; and Thom, The Penicillia, p. 288. 1930. Species reported as related to *P. puberulum* Bainier (*q.v.*) but darker. Known only from description. Possibly based upon some member of *P. roqueforti* series.

P. asperum (Shear) n. comb.

Syn. *Carpenteles asperum* Shear, in Myeologia **26** (1): 104–107,

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figs. 1–3. 1934. Emmons, Mycologia **27:** 146, figs. 15 and 16. 1935..... 263

Scop. atra Zach, in Österr. Bot. Zeitsch. **83:** 184–186, figs. 9 and 10. 1934..... 701

P. atramentosum Thom, in U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, pp. 65–66; fig. 24. 1910. Emended in The Penicillia, pp. 251–252. 1930..... 381

P. atrieolum—a culture was received under this name from Bainier and discussed by Thom (1930) as a variety of *P. rugulosum*. Now regarded as a variant of this species, not warranting varietal recognition..... 653

P. atrobrunneum Cooke, in Grev. **6:** 139. 1877–8. Rav. Fung. Amer. no. 59. Thom, The Penicillia, p. 576. 1930. Not a Penicillium: suggested synonymy—*Haplographium atrobrunneum* Sacc. Syll. **4:** 1886. *Schizocephalum atrobrunneum* (Cooke) Pound and Clements.

P. atro-nitens (*Stysanus*) Saccardo, 1904. In Biourge's Liste Onomastique, p. 100. 1923.

P. atro-viride Dierckx, in Soc. Scient. Brux. **25:** 87. 1901. Also Biourge, Monogr., La Cellule **33:** fasc. 1, p. 199. 1923; and Thom, The Penicillia, p. 279. 1930. Synonym of *P. roqueforti* Thom..... 399

P. atro-viridum Sopp, in Monogr., pp. 149–150, Taf. XVI, fig. 114; Taf. XXIII (XXII corrected), fig. 12. 1912. Thom, The Penicillia, p. 285. 1930. Species probably based upon some member of the *P. roqueforti* series showing dark conidial areas and dark greenish black reverse.... 400

Gliocladium atrum Gilman and Abbott, in Iowa State College Journal Sci. **1:** 305, fig. 40. 1927. By description would seem to represent some Dematiaceous form..... 687

P. aurantio-albidum Biourge, in Monogr., La Cellule **33:** fasc. 1 pp. 197–198; Col. Pl. III and Pl. V, fig. 28. 1923. Thom, The Penicillia, p. 322. 1930. Regarded as a probable synonym of *P. aurantio-candidum* Dierckx.. 442

P. aurantio-brunneum Dierckx, in Soc. Scientif. Bruxelles **25:** 86. 1901; see also, Biourge, La Cellule **33:** fasc. 1, pp. 309–311; Col. Pl. IX and Pl. XV, fig. 85. 1923. Regarded as inseparable from *P. frequentans* Westling... 175

P. aurantio-candidum Dierckx, in Biourge, Monogr., La Cellule **33:** 116–119; Col. Pl. I; Pl. II, fig. 4; and Pl. XXIII, fig. 136. 1923. Thom, The Penicillia, pp. 319–320. 1930..... 442

P. aurantio-griseum Dierckx, in Soc. Scientifique Bruxelles **25:** 88. 1901; Biourge Monogr., La Cellule **33:** 126–128; Col. Pl. I and Pl. II, fig. 8. 1923. Thom, The Penicillia, pp. 401–402. 1930. Some member of the *P. cyclopium* series..... 496

P. aurantio-griseum Dierckx var. *poznaniensis* Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 444–445, Taf. 37. 1927. Thom, The Penicillia, p. 301. 1930. Strain from Zaleski as type represents a member of the Fasciculata approximating *P. cyclopium* Westling..... 496

P. aurantio-violaceum Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 282–284; Col. Pl. X and Pl. XVI, fig. 94. 1923. Thom, The Penicillia, p. 208. 1930..... 192

P. aurantio-virens Biourge, in Monogr., La Cellule **33:** 119–121; Col. Pl. I and Pl. I, fig. 5. 1923. Thom, The Penicillia, pp. 316–317. 1930..... 503

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P. aureo-cinnamomeum Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 213–214; Col. Pl. V, Cart. 61; Pl. VIII, fig. 48. 1923. Assigned by Thom to *Paecilomyces* in The Penicillia, 1930, p. 547.. 689

P. aureo-flavescens Biourge, in Bul. Ass. Anc. El. Ec. Brass. Univ. Louvain, no. 3, p. 32, 1920. Thom, The Penicillia, p. 553. 1930. Biourge, in a letter (1930), stated that this was based upon the same strain as *P. aureoflavum* Biourge (1923, pp. 299–301, etc.), *q.v.*

P. aureo-flavum Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 299–301; Col. Pl. VII and Pl. XII, fig. 69. 1923. Some monoverticillate form with definitely elliptical conidia; not since recognized.

P. aureolimbum Zaleski, in Bul. Acad. Polonaise, Sci.: Math. et Nat. Ser. B, pp. 481–482; Taf. 53. 1927. Thom, The Penicillia, pp. 480–481. 1930. Regarded as probably synonymous with *P. variabile* Sopp..... 644

P. aureum Corda, in Prachtflora, pp. 37–38, Taf. XVIII, figs. 1–3. 1839. Not in Biourge, Monogr., pp. 111–114. 1923. Thom, The Penicillia, p. 469. 1930. Regarded as synonymous with *P. herquei* Bainier and Sartory.... 663

P. aureum Corda, in Biourge, Monogr., La Cellule **33:** 111–114, Col. Pl. I and Pl. I, fig. 2. 1923. Thom, The Penicillia, p. 370. 1930. Synonym of *P. psittacinum* Thom..... 448

P. aureum van Tieghem, in Bul. Soc. Bot. France **24:** 157. 1877; see Thom, The Penicillia, p. 454. 1930. Species not recognizable from data given but usage probably based on some member of the *P. luteum* series.

P. aureum Corda var. *lunzinense* v. Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 157. 1941. The author reported slight variations from the diagnosis of *P. psittacinus* (= *P. aureum* Corda fide Biourge). Culture not available.

Scop. aureus Sartory, in Champignons paras. pp. 680–681. 1922.

P. (*Oospora*) *auridorsum* Biourge, in Monogr., La Cellule **33:** fasc. 1, p. 228; Col. Pl. XII and Pl. XXI, fig. 121. 1923. Thom, The Penicillia, p. 576. 1930. Biourge's organism when grown in culture was not a *Penicillium* and hardly a *Scopulariopsis.*

P. auriftuum Biourge, in La Cellule **33:** fasc. 1, pp. 250–252; Col. Pl. VII and Pl. XI, fig. 64. 1923.
Syn. *P. citrinum* Thom..... 345

P. australicum (Olsen-Sopp) emend. van Beyma, in Antonie van Leeuwenhoek **10:** 53–56, fig. 10. 1945. Van Beyma's description and representative cultures from CBS place this in the *P. terrestre* series as doubtfully separable from *P. terrestre* Jensen..... 453

P. avellaneum Thom and Turesson, in Mycologia **7:** 284–287, figs. 1, 2. 1915; see also Thom, The Penicillia, pp. 446–447, fig. 70. 1930..... 597

P. baarnense van Beyma, in Antonie van Leeuwenhoek **6:** 270–273, figs. 5 and 6. 1939/1940..... 266
Syn. *Penicillium* (*Carpenteles*) *baarnense* van Beyma, *ibid.*

P. bacillosporum Swift, in Bul. Torrey Bot. Club **59:** 221–227; fig. 1, a to g. 1932; also Emmons, Mycologia **27:** 136, figs. 2 and 16. 1935..... 594

P. baculatum Westling, in Svensk Bot. Tids. **4:** pp. 139–145, figs. 1–3. 1910; Arkiv för Botanik **11:** 53, 79–83, figs. 11 and 53. 1911; Biourge, Monogr., La Cellule **33:** fasc. 1, pp. 186–188; Col. Pl. IV

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and Pl. VII, fig. 40. 1923; Thom, The Penicillia, pp. 268–269. 1930. Regarded as a synonym of *P. chrysogenum* Thom. 363

P. baiiolum Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 305–306; Col. Pl. VIII and Pl. XIII, fig. 74. 1923. Regarded as representing *P. purpurrescens* (Sopp) n. comb. 180

P. bainieri Sacc. in Sylloge **22:** 1275. 1913.

Syn. *Scopulariopsis repens* Bainier, Bul. Soc. Mycol. France **23:** 125–127, Pl. XVI, fig. 1–2. 1907.

P. barbae Castellani, cited in editions of the "Manual of Tropical Medicine" by Aldo Castellani and A. J. Chalmers, as found "by us growing on beard of natives of equatorial Africa and Ceylon." Neither a real description of the parasite nor a culture of the mold itself has been seen by us. Thom, The Penicillia, p. 553. 1930. Identity or placement questionable.

P. bassiana (*Spic.*) (Bals.) Vuillemin, 1910. In Biourge's Liste Onomastique, p. 101. 1923.

P. benzianum Sacc., in Sylloge Fungorum **22:** p. 1276. 1913.

Syn. *P. insigne* Sacc. in Ann. Mycol. **5:** 178. 1907. Thom, The Penicillia, p. 519. 1930. The species was described as separated from *P. coccophilum* Sacc. by larger and smooth conidia. Both may be assigned to *Scopulariopsis*.

P. benzoicum Kossowicz in Ztschr. Landw. Versuchswesen, Oesterr, **14:** 69–70. 1911. Thom, The Penicillia, p. 554. 1930. An ascosporic species inadequately described and with ascospores 4 to 7μ by 3 to 4μ—greater variation than in other species—and large yellow perithecia. Probably a variant in the *Aspergillus glaucus* group.

Scop. bertaccini Redaelli (?), cited by Bertaccini in Gior. Ital. Dermat. e Sif. **85:** 783–828, 9 pls. 1934.

P. bertai Talice and Mackinnon, in Ann. Parasitol. Hum. Comp. **7:** 97–106. 1929. A monoverticillate form possibly approximating *P. citreo-viride* Biourge.

P. betae (*Oospora*) Delacr., 1897. In Biourge's Liste *Onomastique*, p. 101. 1923.

P. bialowiezense Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 450–451, Taf. 39, 1927. Thom, The Penicillia, pp. 303–304. 1930. Believed to represent a synonym of *P. brevi-compactum* Dierckx. 410

P. bicolor Fries, in Sys. Myc. **3:** 408. 1829. Thom, The Penicillia, pp. 459–460. 1930. Probably based upon a coremium-forming member of the Biverticillata-Symmetrica.

P. bicolor (*Hapl.*) Grove, 1885. In Biourge's Liste Onomastique, p. 101. 1923.

P. biforme Thom, in U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, pp. 54–55, fig. 18. 1910. Emended in Thom, The Penicillia, pp. 320–322, fig. 45. 1930. 437

P. biforme, Thom var. *lunzinense* Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 169. 1941. Some variant of the *P. chrysogenum-notatum* series is suggested by the description given.

P. biforme Thom var. *vitriolum* Sato, in Jour. Agr. Chem. Soc. Japan **15:** 77. 1939. Bul. pp. 359–369. A culture was received from Sakaguchi in 1940. It proved to be *P. ochro-chloron* Biourge. . 308

P. biourgei Arnaudi, in Boll. Ist. Sieroterapico Milanese **6:** fasc. I,

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pp. 25–27, Pls. 1-2. 1927; also Centbl. f. Bakt. (II) **73:** 321–330. 1928. Thom, The Penicillia, p. 281. 1930. Believed to represent a synonym of *P. roqueforti* Thom..... 401

P. biourgei Dierckx, in Soc. Scient. Brux. **25:** p. 88. 1901; Biourge, Monogr., La Cellule **33:** fasc. 1, p. 167. 1923. Thom, The Penicillia, p. 270. 1930. Known only by description; suspected of approximating *P. casci* Staub since it was reported by both Dierckx and by Biourge to produce black spots on cheese.

P. biourgeianum Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 462–464; Taf. 45 and 48. 1927. Thom, The Penicillia, pp. 296–297. 1930. Believed to represent a synonym of *P. stoloniferum* Thom..... 414

P. blakesleei Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 441–444, Taf. 36. 1927. Thom, The Penicillia, pp. 399–400. 1930. Regarded as representing some member of the *P. viridicatum* series..... 486

Seop. blochii (Matruchot) Vuillemin, in Bul. Soc. Mycol. France **27:** 144–148. 1911.

Syn. *Mastigocladium blochii* Matruchot, in Compt. rend. Acad. Sci. (Paris) **152:** 325–327. 1911.

P. bombycis Sopp, in Videnskapselskapets Skr. I. Mat-Nat. Kl. Kristiania, 1911, no. 2, p. 26. 1912. Thom, The Penicillia, p. 554. 1930. Not recognizable. Species based upon a parasite on the feet of living caterpillars. Conidia reported as 2 to 5μ in diameter and peritheeia (?) 200μ in diameter in green shades. No one has since reported the species with adequate description.

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P. bordzilowskii Morotchkovsky, in Bul. Sci. Rec. Biol. Univ. Kiev. **2:** 71, fig. 2. 1936. Apparently closely related to *P. cyclopium* Westling..... 497

P. bouffardi Brumpt, evidently a typographical error for *Aspergillus bouffardi* Brumpt, cited by Castellani and Chalmers in Manual Tropical Diseases, p. 805. 1913.

P. bovis Doeve, in Ned.-Indische Blad. Diergeneesk **43:** 30–65. 1931. Name provisionally applied to a *Penicillium* isolated from skin ("cascado") lesions of cattle. Inadequately illustrated and not formally described.

P. brachiatum Ellis and Morgan, from the label of a specimen which reads, "Ohio, on ash bark, Morgan, 750." Thom, The Penicillia, p. 554. 1930. Probably some *Gliocladium* or *Clonostachys*; not recognizable from the description.

P. braziliense Thom, in The Penicillia, pp. 483–484, fig. 83. 1930. Identity questionable. Probably some degenerate member of the Biverticillata-Symmetrica.. 644

P. braziliense Thom. var. *lunzinense* Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 157. 1941. Cited by Szilvinyi as "differing from the species in smaller measurements and smoother conidiophores."

P. bredoi Biourge, apparently undescribed—name on tube of Biourge's culture No. 377, marked "Stockholm brewery."

Carpenteles brefeldianum (Dodge) Shear, in Mycologia **26:** 107. 1934. Synonym of *P. brefeldianum* Dodge..... 141

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P. brefeldianum Dodge, in Mycologia **25** (2): 90–104, figs. 1 and 2, Pl. 18 and 19. 1933. Emmons, Mycologia **27:** 145, figs. 13a and b. 1935 141

P. brevicaule var. *album* Thom, in U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, p. 47, fig. 13. 1910. A *Scopulariopsis* with colonies white and conidia rough.. 700

P. brevicaule var. *glabrum* Thom, in U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, pp. 48–49, fig. 16. 1910. A *Scopulariopsis* with colonies white or nearly so and conidia smooth-walled 700

P. brevicaule Sacc. forma *intermedium* D. Sacc. (Mycotheca italica 1726. Centurie XVII, Padua, prior to May 1913). Represented some *Scopulariopsis*.

Scop. brevicaulis (Sacc.) Bainier, in Bul. Soc. Mycol. France **23:** 99–103, Pl. XI, figs. 1–6. 1907..... 697

Syn. *P. brevicaule* Saccardo, in F. ital. t. 893, and Michelia II, p. 547.

P. brevicaulis var. *hominis* Brumpt and Langeron, in Brumpt's Précis de Parasitologie, 2d ed., pp. 902–905. 1913.

Syn. *Penicillium brevicaule*. var. *hominis* Brumpt and Langeron, in Brumpt's Précis de Paras., 1st ed., pp. 838–840, figs. 652–653. 1910. Represents some *Scopulariopsis*.. 700

P. brevi-compactum Dierckx, in Soc. Scient. Brux. **25:** 88. 1901. Biourge Monogr., La Cellule **33:** fasc. 1, pp. 155–157; Col. Pl. II and Pl. III, fig. 16. 1923. Thom, The Penicillia, pp. 295–296. 1930..... 407

P. brevipes Corda, in Icones IV, p. 31, Taf. VII, fig. 93. 1840. Thom, The Penicillia, p. 577. 1930. Not a *Penicillium*: figures and description suggest some *Aspergillus*.

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P. brevipes Sacc., in Patouillard Collection, Farlow Herbarium; specimen labeled "Sur Criquet peleron. Olgerde. 1899. Trabut leg." Thom, The Penicillia, p. 524. 1930. The spores in this specimen were those of some *Scopulariopsis*.

Citromyces brevis Bainier and Sartory, in Bul. Soc. Mycol. France **28:** fasc. 1, 43–45, Pl. II, figs. 1–4. 1912. Not identified. Figures indicate some ramigenous form. 249

P. briandii Vuillemin, cited by von Höhnel, p. 133 of his Fragmente zur Mykologie, 1909. Obviously a misspelling of *P. briardi* Vuillemin, *q.v.*

P. briardi Vuillemin, in Bul. Soc. Mycol. France **20:** 218–221; Pl. 11, fig. 9–10. 1904. Thom, The Penicillia, p. 433. 1930. Some strongly coremiform mold reported by Vuillemin to resemble *Metarrhizium anisopliae* (Metsch.) Sorokin.

P. briosii Carbone, in Atti Ist. Bot. dell Universita Pavia, Ser. II, **14:** pp. 63, 303–308, 321, Tav. XII, figs. 1 and 8. Thom, The Penicillia, pp. 356–357. 1930. Species unidentifiable; possibly one of the Divaricata.

P. brunneo-rubrum Dierckx, in Soc. Scient. Bruxelles **25:** 88. 1901; Biourge, Monogr., La Cellule **33:** fasc. 1, pp. 176–179; Col. Pl. IV and Pl. VI, fig. 36. 1923; Thom, The Penicillia, pp. 267–268. 1930. Regarded as a synonym of *P. cyaneo-fulvum* Biourge.... 372

P. brunneo-violaceum Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 145–147, Col. Pl. II and Pl. IV, fig. 21. 1923. Thom, The Penicillia, pp. 422–423. 1930. Species regarded as inseparable from *P. aurantio-virens* Biourge. 505

P. (*Citromyces*) *brunneo-viride* v. Szilvinyi, in Zentbl. f. Bakt.

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etc. (II) **103:** 145, fig. 4. 1941. Regarded as inseparable from *P. spinulosum* Thom..... 183

Citromyces bruntzii Sartory, in Soc. Biol. (Paris) Compt. Rend. **76:** 605–606. 1914. Believed to approximate *P. spinulosum* Thom. 183

P. burei Pollacci, in Ist. Bot d. R. Univ. Pavia II ser. **18:** 128–129. Tav. XXXI, figs. 4–6. 1921. This was assigned to *Paecilomyces* by Thom in The Penicillia, 1930, p. 548..... 689

P. bussardi (*Hormiscium*) Delacr., 1897. In Biourge's Liste Onomastique, p. 101. 1923.

P. caespitosum E. and E., from the label of an herbarium specimen reading "Maine, Harvey no. 58." Thom, The Penicillia, p. 555. 1930. Some organism near the *P. rugulosum* series.

Mucor caespitosus Linnaeus, in Species Plantarum II, p. 1186. 1753. Based upon Tab. 91, fig. 3, in Micheli, Nova plantarum genera. 1729. Probably synonymous with *P. digitatum* Saccardo.

P. camembert Sopp, in Monogr. pp. 179–180; Taf. XIX, fig. 134; Taf. XXIII, fig. 17–18, 1912. Thom, The Penicillia, p. 313. 1930. Synonym for *P. camemberti* Thom, *q.v.*..... 426

P. camemberti Thom, in U. S. Dept. Agr., Bur. Anim. Ind., Bul. 82, p. 33, fig. 1. 1906; also Bul. 118, p. 50, fig. 16. 1910. The Penicillia, pp. 312–313, figs. 43–44. 1930..... 426

P. camemberti var. *rogeri* Thom, in U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, pp. 52–53, fig. 17. 1910. Synonym of *P. caseicolum* Bainier..... 422

Scop. candelabrum Loubière, in Thèse, pp. 63–64, Pl. VII, figs. 13, 14. 1924..... 700

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Scop. candida (Pers.) Loubière, in Thèse, pp. 64–65, Pl. VIII and IX. 1924. *Nephrospora mangini* Loubière was described and figured as the ascosporic form of *Scop. candida*. Suggested synonyms include: *Monilia candida* Persoon, 1822 and *Aspergillus candidus* Link, 1809..... 695

Scop. candida (Gueguen) Vuill., in Bul. Soc. Myc. France **27:** 143. 1911.

Syn. *Monilia candida* Gueguen 1899, not of Bonorden.

P. candido-fulvum Dierckx, discussed in Biourge, Monogr., La Cellule **33:** fasc. 1, pp. 275–277; Col. Pl. X and Pl. XVII, fig. 98. 1923. Regarded as synonym of *P. frequentans* Westling..... 175

P. candidum Link, in Obs., p. 17. 1809. Thom, The Penicillia, p. 555. 1930. Link's species was never satisfactorily recognized, possibly represented *P. caseicolum* Bainier or some white mutant.

P. candidum Roger, in Biourge Monogr., La Cellule **33:** fasc. 1, pp. 193–194; Col. Pl. III, Pl. V, fig. 27. 1923. This was cited from Roger (Revue Hebdomidaire (Paris) **7:** 334); but Roger regarded his form as *P. candidum* Link, which is unrecognizable. Cultures received as Roger's strains and covered by his patent represent *P. caseicolum* Bainier, q.v..... 425

P. candidum (*Corem.*) Corda, 1837. In Biourge's Liste Onomastique, p. 101. 1923.

P. candidum var. *coremioides* Sacc., in Syll. IV, p. 80. 1886. Thom, The Penicillia, p. 556. 1930. Saccardo transferred *Coremium candidum* Nees to *Penicillium* under this varietal name. Not recognized since it was described.

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P. candidum var. *subcandidum* Peck, in N. Y. State Mus. Rpt. **47:** p. 22. 1894. Thom, The Penicillia, p. 556. 1930. Not identified since described.

P. canditanteum Westling, in Centraalbureau culture list, 1947. Apparently a misspelling of *P. conditaneum* Westling.

P. canescens Sopp, in Monogr. pp. 181–182, Taf. XIX, fig. 136; Taf. XXIII, fig. 28. 1912. Thom, The Penicillia, p. 347, fig. 55. 1930 316

P. canosum Westling, 1911. In Biourge's Liste Onomastique, p. 101. 1923.

P. canum Preuss, in Linnaea **24:** 135. 1851. Thom, The Penicillia, p. 577. 1930. Not identifiable.

P. capitatum Ellis and Galloway, in Herbarium material in Ellis Collection of the New York Botanical Garden. The label reads "on chinch bugs. Nov. 1892." Thom, The Penicillia, p. 556. 1930. Species not since reported—unrecognizable.

P. capitatum (*Haplog.*) (Riess) Sacc., 1886. In Biourge's Liste Onomastique, p. 101. 1923.

P. capreolinum Biourge, in Monogr., La Cellule **33:** fasc. 1, p. 246; Col. Pl. XI and Pl. XVII, fig. 102. 1923; see Thom, The Penicillia, p. 447. 1930. Non-ascosporic; apparently a synonym of *P. avellaneum* T. and T.

Scop. capsici van Beyma, in Antonie van Leeuwenhoek **10:** 50–52, fig. 8. 1945.

P. capsulatum Raper and Fennell, in Mycologia **40:** 528–530, fig. 7. 1948 242

P. carmino-violaceum Dierckx, in Soc. Scientifique Bruxelles **25:** 86. 1901. In Biourge, Monogr., La Cellule **33:** fasc. 1, pp. 281–282; Col. Pl. X and Pl. XVI, fig. 93. 1923. Regarded as synonymous with *P. roseo-purpureum* Dierckx 220

P. carneo-lutescens Smith, in Brit. Myc. Soc. Trans. **22** (3/4): 252–256, Pls. XV and XVI. 1939... 479

P. casei Staub, in Centbl. f. Bakt., etc. (II) **31:** 454–466. 1911. Thom, The Penicillia, p. 270. 1930 401

Scop. casei Loubière, in Thèse, p. 62, Pl. VII, fig. 12. 1924.

P. cascicola Arthault-Berthet, 1905, in Biourge, Monogr., La Cellule, **33:** fasc. 1, p. 101. 1923. In Liste Onomastique, etc. Name only and no description cited or found. Perhaps *P. cascicolum* Bainier, as Arthault-Berthet was working with the French cheese industry at that time.

P. cascicolum Bainier, in Bul. Soc. Mycol. France **23:** 94, Pl. X, fig. 6–10. 1907. Thom, The Penicillia, pp. 310–312, figs. 43A and 44A. 1930..... 422

Scop. castellanii Ota and Komaya, in Dermat. Wochenschr. **78:** 163–165. 1924.

Gliocladium catenulatum Gilman and Abbott, in Iowa State College Jour. Sci. **1:** 303, fig. 37. 1927..... 682

P. caulatum Sopp, in Monogr., p. 103, Taf. II, figs. 7–12. 1912. Thom, The Penicillia, p. 577. 1930. Probable synonym: *Graphium penicilloides* formerly in American Type Culture Collection as No. 1770 from Dr. Caroline Rumbold.

P. cavum Sopp, in Monogr., pp. 192–194; Taf. XXIII, fig. 36. 1912. Thom, The Penicillia, p. 343. 1930. Species not identifiable. Apparently one of the Divaricata.

P. cavum Sopp var. *lunzinense* v. Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 152. 1941. Ap-

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parently a mixed culture; identity not determinable.

Citromyces cesiae Bainier and Sartory, in Bul. Soc. Mycol. France **29:** 148–154, Pl. V, figs. 4–6. 1913. A monoverticillate form regarded by Biourge as *P. roseo-purpureum* Dierckx. A culture from the Bainier Collection, examined by Thom (1930), proved to be *P. cyaneum* (B. and S.) Biourge.

P. cesiae (*Cit.*) Bainier and Sartory. Included in Biourge's Liste Onomastique, p. 101. 1923.

P. charlesii Smith, in Brit. Mycol. Soc. Trans. **18:** 90–91, Pl. V, figs. 7 and 8. 1933..... 248

P. chartarum Cooke, in Popular Science Review **10:** 30–31, Pl. LXVIII, fig. 4. 1871. Thom, The Penicillia, p. 578. 1930.

Syn. *Haplographium chartarum* (Cooke) Sacc., Syll. **4:** 305. 1886.

P. chartarum (*Haplogr.*) (Cooke, 1871). In Biourge's Liste Onomastique, p. 101. 1923.

P. chermesinum Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 284–285; Col. Pl. X and Pl. XVI, fig. 95. 1923. Thom, The Penicillia, pp. 192–193. 1930..... 206

P. chlorinum Fresenius, in Beitr. z. Myk., p. 22, Taf. III. 1850. Thom, The Penicillia, p. 579. 1930. Not a *Penicillium* from the figure perhaps a *Cladosporium*.

P. chlorocephalum Fresenius, in Beitr. z. Myk., p. 20. 1850. Thom, The Penicillia, p. 579. 1930. Not a *Penicillium*.

P. chloro-leucon Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 270–271; Col. Pl. VIII and Pl. XIV, fig. 79. 1923. Thom, The Penicillia, p. 252. 1930. Regarded as a synonym of *P. corylophilum* Dierckx..... 345

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P. chlorophaeum Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 271–273; Col. Pl. VIII and Pl. XIII, fig. 78. 1923; Thom, The Penicillia, pp. 262–263. 1930. Regarded as a synonym of *P. chrysogenum* Thom..... 363

P. chrysitis Biourge, in Monogr., La Cellule **33:** fasc. 1, p. 252; Col. Pl. XI and Pl. XIX, fig. 112. 1923. Thom, The Penicillia, pp. 474–475. 1930. Regarded as probably synonymous with *P. rugulosum* Thom..... 650

P. chrysogenum Thom, in U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, pp. 58–60, fig. 20. 1910; The Penicillia, pp. 261–262. 1930. See also Biourge, Monogr., La Cellule **33:** fasc. 1, pp. 170–172, Col. Pl. IV and Pl. VI, fig. 32. 1923; Westling, Arkiv f. Bot. **11:** 54, 107–108, figs. 23 and 64. 1911..... 359

P. chrysomphalum Biourge, *nomen nudum* in Monogr., La Cellule **33:** fasc. 1, p. 323. 1923. Thom, The Penicillia, p. 556. 1930.

P. chrzaszczi Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 464–466; Taf. 48. 1927. Thom, The Penicillia, p. 337. 1930. Regarded as a synonym of *P. jenseni* Zaleski..... 323

Gliocladium cibotii van Beyma, in Antonie van Leeuwenhoek **10:** 46–48, figs. 4 and 5. 1945.

P. cicadinum v. Höhnel, in Sitzungsber. der Kaiserl. Akad. Wissensch. Wien, Mathem.-Naturw. Klasse 118, Abt. 1, (pp. 131–133 in reprint) 1909. Thom, The Penicillia, p. 578. 1930. Examination of von Höhnel's specimen showed it to be some strain of *Metarrhizium*.

P. cinerascens Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 308–309; Col. Pl. IX and Pl. XIV, fig. 81. 1923. Considered as

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P. fellutanum but showing distinct strain characteristics.... 215

Scop. cinerea Emile-Weil and Gaudin, in Arch. Med. Exp. et Anat. Path., Paris **28:** 458–460, text-fig. 2 and Pl. XII, fig. 2. 1919.

P. cinereo-album (Bonorden, 1851). In Biourge's Liste Onomastique, p. 101. 1923.

P. cinereum Bonorden (Koning, 1903). In Biourge's Liste Onomastique, p. 101. 1923.

P. cinereum (*Syncephalastrum*) Guegen-Bainier. In Biourge's Liste Onomastique, p. 101. 1923.

Syncephalastrum cinereum Gueguen, in Biourge's Monogr., La Cellule **33:** fasc. 1, p. 323, Pl. XXIII, fig. 135. 1923. Thom, The Penicillia, p. 579. 1930. Biourge included this in his *Penicillium* Monograph but noted it to be a *Microaspergillus*. Probably was a form approximating *A. gracilis* Bainier.

P. cinnabarinum Fuckel, in Symbolae Myc. Beitr. Kenntnis der rhein. Zweiter Nachtrag, p. 79. Wiesbaden. 1873. Thom, The Penicillia, p. 556. 1930. Not a *Penicillium*—possibly a *Gliocladium* or related to *P. insigne* Bainier, *q.v.*

P. cinnamomeum (*Geotrichum*) Libert. in Herbario. In Biourge's Liste Onomastique, p. 102. 1923.

P. citreo-lateritium Biourge, in Bul. Ass. Anc. El. Ec. Brass. Univ. Louvain, no. 3, p. 32. 1920. Thom, The Penicillia, p. 557. 1930. Biourge later identified this with *P. sublateritium*, *q.v.*

P. citreo-nigrum Dierckx, in Soc. Scientifique Bruxelles **25:** 86. 1909. Biourge Monogr., La Cellule **33:** fasc. 1, pp. 273–274; Col. Pl. IX and Pl. XV, fig. 87. 1923. Apparently identifiable with *P. citreo-viride* Biourge... 217

P. citreo-nigrum var. *sulfurea*. Unpublished name in Dierckx manuscript, cited as representing *P. citreo-sulfuratum* Biourge in Thom, The Penicillia, p. 198. 1930.

P. citreo-roseum Dierckx, in Soc. Scient. Bruxelles **25:** 86. 1901; Biourge, Monogr., La Cellule **33:** fasc. 1, pp. 182–184; Col. Pl. IV and Pl. VII, fig. 38. 1923; Thom, The Penicillia, pp. 265–266. 1930. Regarded as a synonym of *P. cyanco-fulvum* Biourge..... 373

P. citreo-sulfuratum Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 285–287, Col. Pl. IX and Pl. XV, fig. 86. 1923. Believed to approximate *P. citreo-viride* Biourge..... 217

P. citreo-viride Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 297–299; Col. Pl. IX and Pl. XV, fig. 88. 1923. Thom, The Penicillia, pp. 199–200. 1930..... 215

P. citricolum Bainier and Sartory, in Bul. Soc. Mycol. France **28:** 276–279, Pl. XIII, fig. 1, 2. 1912. Thom, The Penicillia, pp. 481–482. 1930. Regarded as probably synonymous with *P. variabile* Sopp..... 644

P. citricum (*Citr.*) Mazé et Perrier. In Biourge's Liste Onomastique, p. 102. 1923.

Citromyces citricus Mazé and Perrier, in Ann. Inst. Pasteur **18:** 558–559. 1904. Member of the *P. frequentans-spinulosum* complex, but closer diagnosis impossible..... 183

P. citrinum Sopp, in Monogr., pp. 166–167; Taf. XII, fig. 128; Taf. XVIII, fig. 126; Taf. XXIII, fig. 21. 1912; see Thom, The Penicillia, p. 456. 1930. Species not identifiable; possibly a form now

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assignable in the *P. raistrickii* series.

P. citrinum Thom, in U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, pp. 61–63, fig. 22. 1910. Emended in The Penicillia, pp. 256–257, fig. 34. 1930..... 345

"*P. citrinum* Thom", in Biourge, Monogr., La Cellule **33:** fasc. 1, pp. 295–296; Col. Pl. VII and Pl. XI, fig. 65. 1923. Not *P. citrinum* Thom, but a strain or variety of the *P. frequentans* series.

P. cladosporioides Fresenius, in Beitrage zur Mykologie, Taf. III, pp. 22–23, figs. 23–28. 1850–3. Thom, The Penicillia, p. 579. 1930. Probably some *Cladosporium*.

P. clavariaeforme (*Penicilliopsis*) Solms-Laubach, 1886. In Biourge's Liste Onomastique, p. 102. 1923.

P. claviforme Bainier, in Bul. Soc. Mycol. France **21:** 127, Pl. XI, figs. 8–11. 1905; Saccardo, Syll. fung. **18:** 520; Thom, U. S. Dept. Agr., Bur. Anim. Ind., Bul. **118:** 44, fig. 10. 1910; Thom, The Penicillia, pp. 432–433, fig. 68. 1930..... 549

P. claviforme Bainier var. *minus* Biourge, La Cellule **36:** 454. 1925. Thom, The Penicillia, p. 433. 1930. A varietal name without description applied to a culture sent to Biourge by H. G. Derx of Delft.

Coremium claviforme (Bainier) Peck, in New York State Mus. Bul. 131, p. 16. 1909. Name applied to a culture from Thom. Synonym of *P. claviforme* Bainier... 549

P. clavigerum Demelius, in Verhandl. Zool. Bot. Gesellsch. Wien. **72:** 74–75, fig. 4. (1922) 1923. Thom, The Penicillia, p. 427. 1930..... 553

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Isaria clonostachoides Pritchard and Porte, in Phytopathology **12:** 167–172, fig. 1, Pl. XII. 1922. Regarded as possibly representing some *Gliocladium*..... 680

P. coccophilum Sacc. in Ann. Mycol. **5:** 178. 1907. Thom, The Penicillia, p. 526. 1930. This species was some *Scopulariopsis*.

P. coeruleum (*Citro.*) Bain. and Sart. 1912, a usage cited by Biourge in his Liste Onomastique (1923, p. 102) without additional reference.

P. coeruleum (*Citro.*) Sopp, in Biourge's Liste Onomastique, p. 102. 1923.

Citromyces coeruleus Sopp, in Monogr., pp. 110–112, Taf. XIII, fig. 95, Taf. XXII, fig. 1. 1912. Thom, The Penicillia, p. 176. 1930. A monoverticillate form producing abundant sclerotia. Not identified since described. Probably a member of the *Penicillium thomii* series.

P. coffeicolor B. and Br., in Ann. N. H. n. 1614. Thom, The Penicillia, p. 527. 1930. This was perhaps a *Scopulariopsis*.

P. columnare Thom, in The Penicillia, pp. 214–215. 1930. Probably represented a nutrient deficient strain in the *P. frequentans* series..... 176

P. commune Thom, in U. S Dept. Agr., Bur. Anim. Ind., Bul. 118, p. 56, fig. 19. 1910; also Thom, The Penicillia, pp. 324–325, figs. 46 and 47. 1930..... 439

P. commune Thom var. *luzinense* v. Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 162. 1941. Without the type culture definite placement is not possible.

Scop. communis Bainier, in Bul. Soc. Mycol. France **23:** 125–127, Pl. XVI, figs. 3–6. 1907.

Scop. communis Bainier var. *luzi-*

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nense Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 173. 1941.

P. conditaneum Westling, in Arkiv för Botanik **11:** 52, 63–65, figs. 46 and 2. 1911. Thom, The Penicillia, p. 386. 1930. Probably synonymous with *P. cyclopium* Westling..... 496

P. congolense Dierckx, in Soc. Sci. Brux. **25:** 87. 1901. Thom, The Penicillia, p. 557. 1930. Never since recognized with certainty.

P. constanti Bainier. A misspelling by Smith and Ramsbottom of *P. constantini* Bain., in Trans. Brit. Myc. Soc. **5:** 163. 1915.

P. convitaneum Westling. Name on culture from Pribram, presumably a corruption of *P. conditaneum* Westling.

P. coremioides Sacc., cited in Biourge Monogr., La Cellule **33:** fasc. 1, p. 102. 1923. *P. roseum* var. *coremioides* Kickx in Sacc. Syll. IV, p. 83. 1886; cited by Saccardo from Kickx Flore Crypt. Flandres, Vol. 2, p. 306. 1867. Thom, The Penicillia, p. 557, 1930. Saccardo's usage based upon error; to be dropped.

P. corylophilum Dierckx, in Soc. Scientifique Bruxelles **25:** 86. 1901. In Biourge, Monogr., La Cellule **33:** fasc. 1, pp. 266–267; Col. Pl. IX and Pl. XIV, fig. 83. 1923. Thom, The Penicillia, p. 254. 1930..... 341

P. corymbiferum Westling, in Arkiv för Botanik **11:** 56, 92–95; figs. 16, 58. 1911. Thom, The Penicillia, pp. 423–425. 1930..... 540

Scop. costantini (Bainier) Dale, in Ann. Mycol. **12:** 57. 1914..... 701

Syn. *Synpenicillium album* Costantin, Bul. Soc. Mycol. France **4:** 62–68, Pl. XIV, figs. 10–17. 1888.

P. costantini Bainier, in Bul. Soc. Mycol. France **22:** 205–207, Pl. XI, figs. 1–6. 1906.

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P. crassum Sopp, in Monogr., p. 147–148, Taf. XVI, fig. 111; Taf. XXII, fig. 15. 1912. Thom, The Penicillia, pp. 297–298. 1930. Believed to represent a synonym of *P. brevi-compactum* Dierckx..... 410

P. crateriforme Gilman and Abbott, in Iowa State College Jour. Sci. **1:** no. 3, p. 293, fig. 28. 1927. Thom, The Penicillia, p. 475. 1930. Regarded as probably synonymous with *P. rugulosum* Thom..... 650

P. crevicaule, in Plant Physiol. **7** (4): 630–633. 1932. A misprint for *P. brevicaule*.

P. crocco-hyacinthinum Biourge, in Bul. Ass. Anc. El. Ec. Brass. Univ., Louvain, no. 3, p. 32, 1920. Thom, The Penicillia, p. 557. 1930.

Syn. *P. implicatum* Biourge, *fide* letter from Biourge.

Scop. croci van Beyma, in Antonie van Leeuwenhoek **10:** 52–53, fig. 9. 1945..... 701

P. crustacea (*Oosp.*) Bulliard. In Biourge's Liste Onomastique, p. 102. 1923.

P. crustaceum Fries, in Sys. Myc. **3:** 407. 1829. Thom, The Penicillia, p. 406. 1930. *P. expansum* series, possibly closest to *P. crustosum* Thom..... 515

P. crustaceum β coremium Fries, in Sys. Myc. **3:** 407. 1829. Syn. *P. expansum* Link.

P. crustaceus (*Mucor*) L., 1753. In Biourge's Liste Onomastique, p. 102. 1923.

P. crustatum in Thom, The Penicillia, p. 558. 1930. Misspelling for *P. crustaceum* in a paper by Castellani.

P. crustosum Thom, in The Penicillia, p. 399. 1930..... 516

P. cupricum Trabut, in Bul. Soc. Bot. France **42:** 451–455. 1895. See also De Seynes, *ibid.*, p. 482–485,

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and Bul. Soc. Mycol. France **15:** 21. 1899. Thom, The Penicillia, p. 558. 1930. Recently tested copper tolerant forms have been assigned to *P. ochrochloron* Biourge. Trabut's strain is not known.

P. cuprophilum Sato, in Jour. Agr. Soc. Japan **15:** 77. 1939. Bul., pp. 359–369. A culture received from Sakaguchi in 1940 proved to be *P. ochro-chloron* Biourge.. 308

P. curtipes Berkeley, in Ann. and Mag. Nat. Hist., Ser. 2, **2:** 380–383, Pl. XI. 1848. Thom, The Penicillia, p. 580. Branching chains of spores exclude this from *Penicillium*.

P. cyaneo-carmineum Biourge, in Bul. Ass. Anc. El. Ec. Brass. Univ., no. 3, p. 32, Louvain, 1920. Thom, The Penicillia, p. 558. 1930. *Nomen nudum*. Biourge, in letter of May 1930, reported culture lost, hence not described.

P. cyaneo-fulvum Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 174–176; Col. Pl. IV and Pl. VI, fig. 34. 1923. Thom, The Penicillia, p. 267. 1930..... 371

P. cyaneum (B. and S.) Biourge, in Monograph, Liste Onomastique, La Cellule **33:** fasc. 1, p. 102. 1923. Emend. Thom, in The Penicillia, pp. 226–228. 1930... 244

Syn. *Citromyces cyaneus* Bainier and Sartory, in Bul. Soc. Mycol. France **29:** 157–161; Pl. IV, fig. 4. 1913..... 244

P. cyclopium Westling, in Arkiv för Botanik **11:** 55–56, 90–92, figs. 15 and 57. 1911. Thom, The Penicillia, pp. 384–386. 1930..... 493

P. cyclopium West. var. *echinulatum* n. var..... 497

P. cyclopodium Westling is a misspelling of *P. cyclopium* Westling in DuPlessis, Univ. of S. Africa, Dept. Agr. and For. Sc., Bul. **151:** 12. 1936.

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P. daleae Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 495–496; Taf. 57. 1927. Thom, The Penicillia, p. 360. 1930..... 296

Scop. danica van Beyma, in Zentbl. f. Bakt. etc. (II) **99:** 391, fig. 5. 1939..... 701

P. decumbens Thom, in U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118; p. 71, fig. 28. 1910. See Biourge, Monogr., La Cellule **33:** fasc. 1, pp. 287–288; Col. Pl. IX and Pl. XV, fig. 89. 1923. Thom, The Penicillia, pp. 197–198, fig. 24. 1930..... 209

P. decumbens (*Spicaria*) Oudem. and Kon. 1902. In Biourge's Liste Onomastique, p. 102. 1923.

P. deformans Sopp, in Monogr., pp. 184–186; Taf. XXI, fig. 145 (196 in text); Taf. XXIII, fig. 32. 1912. Thom, The Penicillia, p. 558. 1930. Species probably approximates *P. sclerotiorum* van Beyma.

P. delacroixii Saccardo. In Biourge's Liste Onomastique, p. 102. 1923.

P. delicatum (*Haplogr.*) (B. and Br.), 1859. In Biourge's Liste Onomastique, p. 102. 1923.

Gliocladium deliquescens Sopp, in Monogr., pp. 89–93, Taf. I, figs. 1–6. 1912..... 686

P. deliquescens (*Gliocl.*) Sopp, 1912. In Biourge's Liste Onomastique, p. 102. 1923.

P. densa (*Spicaria*) (Giard) Vuillemin, 1904. In Biourge's Liste Onomastique, p. 102. 1923.

P. dermatophagum (*Coroll.*) Sopp, 1912. In Biourge's Liste Onomastique, p. 102. 1923.

Syn. *Corollium dermatophagum* Sopp, in Monogr., pp. 99–103, Taf. X, fig. 108; Taf. XIII, fig. 45. 1912. Probably some *Paecilomyces*..... 689

P. desciscens Oudemans, in Arch.

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Neerlandaises des Sc. Exactes et Nat. 288 (289?), Tab. XXIV, figs. 1–5. 1902. See also Oudemans in Nederl. Kruidk. Arch. Ser. 3, **2:** 907. 1903; Westling, Arkiv för Botanik **11:** 147. 1911; and Thom, The Penicillia, pp. 491–492. 1930. Believed to represent some atypical member of the Biverticillata-Symmetrica.

P. dierckxii Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 313–315; Col. Pl. X and Pl. XVI, fig. 91. 1923. Variant member of *P. fellutanum* 215

P. difformis (*Stys.*) Oudemans, 1902. In Biourge's Liste Onomastique, p. 102. 1923.

Monilia digitata Fries, in Syst. Mycol. **3:** 407. 1829. Probable synonym of *P. digitatum* Sacc.

Monilia digitata Persoon, in Synopsis Methodica Fungorum, Part II, p. 693. 1801. Synonym of *P. digitatum* Saccardo *q.v.*

P. digitatoides Peyronel, in I germi atmosferici dei funghi con micelio, p. 22, Padova. 1913. Thom, The Penicillia, p. 245. 1930. Peyronel admits that this species was only a cultural form of *P. digitatum* Sacc.

P. digitatum Sacc., in Mycotheca Italica, No. 986, Herbarium, U. S. Dept. Agr.; in Sylloge Fungorum, Vol. IV, p. 78. 1886; in Fungi Italici, No. 894. Thom, The Penicillia, pp. 242–245, figs. 29–30. 1930..... 386

P. digitatum Sacc. var. *californicum* Thom, in The Penicillia, p. 245. 1930. Variety based upon a white mutant of the species showing the same activities as *P. digitatum*..... 390

P. divaricatum Thom, in U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, pp. 72–73, fig. 29. 1910; also The Penicillia, pp. 544–546. 1930..... 691

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Syn: *Paecilomyces varioti* Bainier. 691

P. divaricatum (?) Thom, in Biourge, Monogr., La Cellule **33:** fasc. 1, pp. 224–225; Col. Pl. VI and Pl. X, fig. 59. 1923. Thom, The Penicillia, p. 530. 1930. Biourge misinterpreted this to represent some *Scopulariopsis*.

Spicaria divaricata (Thom) Gilman and Abbott, in Iowa State Col. Jour. Sci. **1:** 301. 1927.

P. divergens Bainier and Sartory, in Bul. Soc. Mycol. France **28:** 270–276, Pl. XIII, figs. 3–6. 1912. Thom, The Penicillia, pp. 427–429, fig. 65. 1930. Synonym of *P. granulatum* Bainier..... 546

Scop. diversispora van Beyma, in Zentbl. f. Bakt. etc. (II) **96:** 430–432. 1937..... 701

P. dubiosum Wehmer, cited only by Doebelt, in Ann. Mykol. **7:** 315–338. 1909. Thom, The Penicillia, p. 559. 1930. *Nomen nudum*.

P. diversum Raper and Fennell, in Mycologia **40:** 539–541, fig. 11. 1948..... 653

P. diversum var. *aureum* Raper and Fennell, in Mycologia **40:** 541–542, fig. 11. 1948..... 655

P. duclauxi Delacroix, in Bul. Soc. Myc. France **8:** 107, Pl. VII. 1891. Thom, U. S. Dept. Agr. Bur. Anim. Ind., Bul. 118: 42, fig. 9. 1910; Thom, The Penicillia, pp. 458–459, fig. 73. 1930.. 610

P. duponti Griffon and Maublanc emend. Emerson. Original description in Bul. Soc. Mycol. France **27:** 68–74, figs. 4–8. 1911. 573

P. eborinum Sasaki, in Fukuoka Acta Medica **32:** 1572–1644, illust. (In Japanese). German summary, *ibid.* pp. 97–98. 1939. Species inadequately described but appears to represent some *Scopulariopsis* with small conidial structures. Isolated from a case of otomycosis.

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P. echinatum Dale, in Biourge's Monogr., La Cellule **33:** fasc. 1, p. 278, Col. Pl. XI, and Pl. XVIII, fig. 104. 1923. Synonym of *P. nigricans* (Bainier) Thom, *q.v.* 325

P. echinatum Rivolta, in Parass. veget. p. 451, Tav. VI, figs. 150–151. 1873.

Syn. *Haplographium echinatum* (Riv.) Sacc. in Sylloge **IV:** 307. 1886. Thom, The Penicillia, p. 580. 1930.

P. echinatum (*Hapl.*) (*Rivolta*) Sacc., 1886. In Biourge's Liste Onomastique, p. 102. 1923.

P. echinulatum Dale. Name appears in Biourge's "Liste Onomastique" Monograph, p. 102. 1923. Apparently a misspelling of *P. echinatum* Dale.

P. egyptiacum van Beyma, in Zentbl. f. Bakt. etc., (II) **88:** 137–138, figs. 6 and 7. 1933. Sabet, Zentbl. f. Bakt. etc., (II) **94:** 97–102, figs. 1-6. 1936 269

P. ehrlichii Klebahn, in Ber. deut. bot. Gesell. **48** (9): 374–389, figs. 1–14. 1930. Emmons, Mycologia **27:** 145, figs. 14 and 16. 1935 146

P. elasticae (*Corem.*) Koorders, 1907. In Biourge's Liste Onomastique, p. 102. 1923.

P. elegans Corda, in Icon. II, Table XI, fig. 74, p. 18. 1838. Thom, The Penicillia, p. 549. 1930. Assigned to *Paecilomyces* by Gilman and Abbott (1927).

Syn. *Spicaria elegans* Harz.

P. elegans (*Spic.*) Corda, 1838, Harz, 1871. In Biourge's Liste Onomastique, p. 102. 1923.

P. elegans Sopp, in Monogr., pp. 144–145; Taf. XVI, fig. 112; Taf. XXII, fig. 13. 1912. Thom, The Penicillia, p. 470. 1930. Regarded as synonymous with *P. herquei* Bainier and Sartory. 663

P. elegantula (*Isaria*) C. Bakt. 26, 469. In Biourge's Liste Onomastique, p. 102. 1923.

P. elongatum Bainier, in Bul. Soc. Mycol. France **23:** 17–18; Pl. V, figs. 1–7. 1907; Thom, The Penicillia, p. 485. 1930. Synonym of *P. tardum* Thom..... 651

P. elongatum Dierckx, in Soc. Scientifiques Bruxelles **25:** 87. 1901. Thom, The Penicillia, pp. 411–412. 1930. Synonym of *P. expansum* Link 515

P. epigeum B. and C., in Grevillea **3:** 111–112, March 1875; cited as *P. epigaeum* B. and C., in Saccardo Syl. **4:** 82. 1886. Thom, The Penicillia, p. 559. 1930. Species described as fulvous with monoverticillate penicilli and conidia 13 to 15 μ. Not reported again, hence unrecognized here.

P. eptseinii Lindau, in Deutsch. Krypt. Flora, Pilze **8:** 166. 1904–1907. Synonym of *P. cascicolum* Bainier..... 422

P. equinum van Beyma, in Zentbl. f. Bakt. etc. (II) **96:** 421–423, figs. 1 and 2. 1937. Species described as ascosporic in terms which would relate it to the *Carpenteles* series. A strain received from the Centraalbureau in 1945 under this name failed to produce perithecia and approximated *P. terrestre* Jensen.

P. erectum Bainier, in Bul. Soc. Mycol. France **23:** 13, Pl. III, figs. 1–16. 1907. Thom, The Penicillia, p. 295. 1930. Believed to represent a synonym of *P. stoloniferum* Thom 413

Paecil. erectus Demelius, in Verhandl. Zool.-Bot. Gesellsch. Wien. **72:** 78–79, figs. 7 and 8. (1922) 1923. Thom, (1930, pp. 486–487) regarded it as doubtfully a member of the Biverticillata Symmetrica.

P. eriopoda (*Isaria*) Bainier, 1913.

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In Biourge's Liste Onomastique, p. 102. 1923.

P. euglaucum van Beyma, in Antonie van Leeuwenhoek **6:** 267–270, figs. 3 and 4. 1939/1940..... 269

Syn. *Penicillium* (*Carpenteles*) *euglaucum* van Beyma, *ibid.* Type culture indistinguishable from *P. baarnense* van Beyma and species regarded as synonym..... 269

P. exiguum Bainier, in Bul. Soc. Mycol. France **23:** 96, Pl. X, fig. 5. 1907. Thom, The Penicillia, pp. 492–493. 1930. Species known only from description. Thom (1930, p. 492) regarded it as probably some symmetrically biverticillate form.

Citromyces exiguus Bainier and Sartory, in Biourge's Monogr., La Cellule **33:** fasc. 1, p. 102, in Liste Onomastique, is apparently a mistake for *Aspergillus gracilis* var. *exiguus* of B. and S. of their 1912 paper.

P. expansum Link, in Obs., p. 17. 1809. Emended Thom in U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, pp. 27–28, fig. 1. 1910; also Thom, The Penicillia, pp. 402–405, figs. 60 and 61. 1930... 512

P. expansum Thom, in Biourge, Monogr., La Cellule **33:** fasc. 1, pp. 139–141; Col. Pl. II and Pl. III, fig. 15. 1923. Thom, The Penicillia, pp. 406–407. 1930. Not *P. expansum* Link as reported by Thom in publications of 1910 and 1930.

P. farinosa (*Isaria*, *Spic.*), Vuillemin, 1904. In Biourge's Liste Onomastique, p. 102. 1923.

P. fasciculatum Sommerfelt, in Suppl. Florae Lapponicae, p. 342. 1826. Thom, The Penicillia, p. 559. 1930. No interpretation appears warranted.

P. fastigiatum nomen nudum, G. F. Atkinson, no. 14910 in Flora Cayuga Lake Basin, New York: Cornell University. Thom, The Penicillia, p. 465. 1930. Probably *P. funiculosum* Thom.

P. felina (*Isaria*, *Spic.*) (D.C.) Vuillemin, 1904. In Biourge's Liste Onomastique, p. 102. 1923.

P. fellutanum Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 262–264; Col. Pl. XIII and Pl. XXIII, fig. 133. 1923. Thom, The Penicillia, pp. 198–199, fig. 25. 1930..... 212

Gliocladium fimbriatum Gilman and Abbott, in Ia. State College Jour. Sci. **1:** 304, fig. 38. 1927.. 684

Spicaria fimetaria Moesz, in Bot. Koslem **19:** 58, fig. 9. 1921. Figures suggest *Paecilomyces varioti* Bainier..... 689

P. fimetarius (*Stys.*) Karsten, 1887. In Biourge's Liste Onomastique, p. 102. 1923.

P. fimicola (*Corem.*) Marchal, 1895. In Biourge's Liste Onomastique, p. 103. 1923.

Scop. fimicola (Cost. and Matr.) Vuillemin, in Bul. Soc. Mycol. France **27:** 137–152. 1911.

Syn. *Monilia fimicola* Costantin and Matruchot.

P. finitimum Preuss, in Fungi Hoyerswerda no. 118, Linnaea **24:** 134. 1851. Thom, The Penicillia, p. 580. 1930.

Syn. *Haplographium finitimum* (Preuss) Sacc.

P. finitimum (*Haplogr.*) Preuss, 1851. In Biourge's Liste Onomastique, p. 103. 1923.

P. firmum Preuss, in Fungi Hoyerswerda, Linnaea **24:** 136. 1851. Thom, The Penicillia, p. 580. 1930. Excluded from *Penicillium* by its fuscous conidiophores; never since identified.

P. flavi-dorsum Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 290–291; Col. Pl. VIII and Pl. XIII, fig. 73. 1923. Regarded as syn-

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onymous with *P. frequentans* Westling..... 176

P. flavido-marginatum Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 150–152; Col. Pl. III; Pl. IV, fig. 24. 1923. Regarded as approximating *P. aurantio-virens* Biourge 505

P. flavo-cinereum Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 293–295; Col. Pl. VIII and Pl. XIII, fig. 76. 1923. Regarded as *P. spinulosum* Thom. 184

P. flavo-fuscum Biourge, in Bul. Ass. Anc. El. Ec. Brass. Univ., Louvain, no. 3, p. 32. 1920. Thom, The Penicillia, p. 560. 1930. *Nomen nudum*—species never adequately described.

P. flavo-glaucum Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 130–132; Col. Pl. I and Pl. II, fig. 10. 1924. Thom, The Penicillia, p. 386. 1930. Probably approximates *P. crustosum* Thom..... 518

P. flavo-virens Cke. and Mass. in Grev. **20:** 106. 1891. Thom, The Penicillia, p. 581. 1930. Not identifiable from the data given.

Acaulium flavum Sopp, in Monogr., pp. 53–56, Taf. IX and XI, figs. 76–79. 1912. Some *Scopulariopsis*; perithecia reported.

Gliocladium flavum van Beyma, in Verh. Akad. Wet. Amst., II Sect. **26:** 5–10, 2 figs. 1928.

P. flavum El. and Em. Marchal, in Bul. Soc. Roy. Bot. Belgique, T. 54, (Ser. 2 T. IV), p. 129. 1921. Thom, The Penicillia, p. 550. 1930. Species known only from description. Probably a species of *Paecilomyces*..... 689

P. flavum (*Acaul.*) Sopp. 1912. In Biourge's Liste Onomastique, p. 103. 1923.

P. flexuosum Dale, in Ann. Mycol. **24:** 137. 1926. Previously published in Biourge, Monogr., La Cellule **33:** fasc. 1, pp. 264–265; Pl. XIX, fig. 110. 1923. Incorrectly cited *P. flexuosum* Westling by Biourge, *ibid.*, p. 103 and Col. Pl. XI. Synonym of *P. urticae* Bainier..... 534

P. flexuosum Preuss, in Linnaea **24:** 135. 1851. Thom, The Penicillia, p. 581. 1930. Not a *Penicillium*: Saccardo puts it in *Haplographium* (Syll. Fung. IV, p. 307. 1886).

P. flexuosum Westling. In Biourge's Liste Onomastique, p. 103. 1923.

P. fluitans Tiegs, in Ber. deut. bot. Gesellsch. **37:** 499–501. 1919. Probably a member of the *P. frequentans* series..... 176

P. fluorescens Laxa, discussed but no description cited in Zentbl. f. Bakt., etc. (II) **86:** 162–163. 1932. Examination of type culture indicates species based upon striking cultural variant of *P. chrysogenum* Thom..... 364

Monilia formosa Sakaguchi, Inoue, and Tada, in Zentbl. f. Bakt. etc. (II) **100:** 302–307. 1939. Species based upon a culture approximating *Paecilomyces varioti* Bainier.

Citromyces fötens Sopp, in Monogr., pp. 113–115, Taf. XIII, fig. 96; Taf. XXII, fig. 2. 1912. Believed to approximate *P. purpurrescens* (Sopp) n. comb.

P. frequentans Westling, in Arkiv för Botanik **11:** pp. 58, 133–134, figs. 39, 78. 1911. In Biourge's Monogr., La Cellule **33:** fasc. 1, pp. 292–293; Col. Pl. X and Pl. XVII, fig. 99. 1923. Thom, The Penicillia, pp. 216–217. 1930..... 172

P. (*Citrom.*) *frequentans* Westling var. *P. citrinum* Thom sensu Biourge in v.Szilvinyi Zentbl. f. Bakt. etc. (II) **103:** 146–147. 1941. This is an impossible

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usage referring to a culture of uncertain identity.

P. friemanthe, name applied to a culture distributed by Pribram, and at one time by the Centraalbureau. No description known. Culture examined by Thom under this name (in 1924) approximated *P. terrestre* Jensen.

P. fructigenum Takeuchi, in Bul. Sci. Fak. Terkult. Kjusu Imp. Univ. **3:** 333–449, illus. 1929. Probably based upon a variation of *P. expansum* Link or some related fasciculate form. Conidia reported as globose—not elliptical.

P. fuliginea (*Catenularia*) Saïto, 1904. In Biourge's Liste Onomastique, p. 103. 1923.

Byssochlamys fulva Olliver and Smith, in Jour. of Bot. **72:** 196–197, Pl. 602. 1933..... 692

Acaulium fulvum Sopp, in Monogr., pp. 67–70, Taf. IX, figs. 81–84; Taf. XII, fig. 80. 1912. Possibly represented some *Isaria* or *Paecilomyces*.

P. fulvum Rabenhorst, in Krypt. Fl. 1 aufl. 1, 92. 1844. Was given as a synonym of *Rhodocephalus aureus* Corda, in Icones III, p. 12, fig. 33. 1839. Thom, The Penicillia, p. 581. 1930. Corda's figure might have been an *Aspergillus* or some monoverticillate *Penicillium*.

P. fulvum (*Rhoceph*) Rabenh., 1844. In Biourge's Liste Onomastique, p. 103. 1923.

P. fumosus (*Aspergillops.*) Sopp. In Biourge's Liste Onomastique, p. 103. 1923.

P. funiculosum Thom, in U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118: 69, fig. 27. 1910. Thom, The Penicillia, pp. 464–465, fig. 77. 1930..... 616

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Scop. fusca Zach, in Österr. Bot. Zeitsch. **83:** 173–186. 1934..... 700

P. fuscipes Preuss, Fungi Hoyerswerda no. 123, in Linnaea **24:** 136. 1851. Thom, The Penicillia, p. 581. 1930.

Syn. *Haplographium fuscipes* Sacc. in Syll. **IV:** 307. 1886; and Centbl. f. Bakt. etc. (II) **20:** 178. 1908.

P. fusco-glaucum Biourge, in Monogr., La Cellule **33:** 128–130, Col. Pl. I and Pl. II, fig. 9. 1923. Thom, The Penicillia, pp. 325–326. 1930. Species regarded as a probable synonym of *P. commune* Thom.

P. fusco-glaucum Biourge var. *lunzinense* v. Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 164. 1941. Probably a variant strain of *P. terrestre* or near but no culture available for examination.

P. fuscum (Sopp) n. comb..... 226

Syn. *Citromyces fuscus* Sopp.

Citromyces fuscus Sopp, in Monogr., pp. 120–122, Taf. XIV, fig. 100; Taf. XXII, fig. 6. 1912. Thom, The Penicillia, p. 180. 1930. See *P. fuscum* (Sopp) n. comb... 226

P. geophilum Oudemans, in Arch. Neerlandaises, p. 288; Tab. XXV, figs. 1–5. 1902. Possibly a member of the *P. frequentans* series but with measurements larger than in typical strains.

P. gibbelluloides Arnaud and Barthelet, in Ann. Epiphytis et Phytogenetique **1:** 135, fig. 8. 1934/1935. This name was tentatively applied to a much branched conidial structure (figured), possibly representing a *Haplographium*, observed from the chrysalid of a lepidopterous insect in Madagascar.

P. gilmanii Thom, in The Penicillia, pp. 345–346. 1930. Type strain

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lost and species no longer identifiable. Apparently some divaricate form with numerous monoverticillate penicilli. Thom applied this name to a strain received from Gilman and Abbott as *P. cinerascens* Biourge.

P. gilvum Sopp, in Monogr., pp. 167–169, Taf. XI, fig. 130; Taf. XVIII, fig. 125; Taf. XXIII, fig. 21. 1912; see Thom, The Penicillia, p. 454. 1930. Species not identifiable; peritheeia reported but not ascospores; probably some member of the *P. luteum* series.

P. giordanoi Vuillemin, in Champ. Parasit. p. 62. 1931.

Syn. *P. glaucum* Giordano, in Ann. Med. Nav. Colon. **24:** 567. 1918. Original paper not seen.

Citromyces glaber Wehmer, in Beitr. z. Kennt. einh., Pilze I, p. 24; Taf. I, figs. 14–24. 1893. Regarded as *P. frequentans* Westling..... 176

P. glaber (*brum*) (*Citr.*)? Wehmer. In Biourge's Liste Onomastique, p. 103. 1923.

P. glabrum series, in Thom, The Penicillia, p. 215. 1930. Forms contained therein are included in *P. frequentans* Westling of this Manual..... 172

P. glabrum (Wehmer) Westling, in Arkiv för Botanik **11:** no. 1, pp. 131–132, fig. 77. 1911. Regarded as *P. frequentans* Westling..... 176

P. gladioli Machacek, in Quebec Soc. for the Protection of Plants Ann. Rpt. **19:** 77–86. (1927) 1928. Independently published under the same specific name by McCulloch and Thom, Science **67:** 216–217. 1928. Thom, The Penicillia, pp. 381–383, fig. 58. 1930..... 471

P. glandicola (*Corem.*) Oudemans, 1903. In Biourge's Liste Onomastique, p. 103. 1923.

Floccaria glauca Greville, in Scottish Flora, Pl. 301, figs. 1–4. 1823–1828. Synonym of *P. expansum* Link..... 512

P. glauco-ferugineum Sopp, in Monogr., pp. 152–153, Taf. XVII, fig. 116, Taf. XXII, fig. 9. 1912. Thom, The Penicillia, p. 364. 1930. Species not identifiable; inadequately described and figured.

P. glauco-griseum Sopp, in Monogr., pp. 189–190; Taf. XXI, fig. 147; Taf. XXIII, fig. 35. 1912. Thom, The Penicillia, p. 346. 1930. Species not identifiable, suggests *P. raistrickii* Smith but no sclerotia reported.

P. glauco-ochraceum Preuss, in Linnaea **24:** p. 135, 1851. Thom, The Penicillia, p. 550. 1930. Species not recognizable.

P. glauco-ochraceum Sopp. In Biourge's Liste Onomastique, p. 103. 1923.

P. glauco-roseum Demelius, in Verhandl. Zool. Bot. Gesellsch. Wien. **72:** 72, fig. 3. (1922) 1923. Thom, The Penicillia, p. 344. 1930. Regarded as a synonym of *P. janthinellum* Biourge..... 303

Coremium glaucum Corda, in Icones V, fig. 31. 1842. Synonym of *P. expansum* Link.

Coremium glaucum Link, in Observationes, p. 19. 1809. Synonym of *P. expansum* Link..... 512

P. glaucum Link, in Obs., p. 17, 1809. Thom, The Penicillia, p. 560. 1930. Frequently used for any green *Penicillium*; no one knows what form was described by Link.

P. glaucum Link, in Species Plantarum Ed. 4, Vol. 6, p. 70. 1824. In part synonymous with *P. expansum* Link (1809)..... 512

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P. glaucum Link, in Sopp Monogr., pp. 140–141, quoted from his book Uber Kasevergarung, Christiania, 1905. I. Sauermilchkase, p. 68. 1912. Thom, The Penicillia, p. 561. 1930. Possibly *P. roqueforti* Thom.

P. glaucum Link *fide* Wehmer, in Beitr. z. Kennt. Einh., Pilze II, 1 p. 76–77; Taf. I, fig. 5 and probably figs. 6 and 7; Taf. III, figs. 16–22. 1895. Thom, The Penicillia, p. 407. 1930. Not identifiable but probably *P. expansum* Link..... 515

P. glaucum Lk. var. *crustaceum* Fr., in Farlow Herbarium labeled "63. Ch. Spegazzini, Fungi Guaranitici. (1885–1889). Speg. 11. no. 381. Skin of citrus fruit. Guarpi." Thom, The Penicillia, p. 562. 1930. One may guess *P. digitatum* Sacc.

P. glaucum f. *epimyces* Sacc., in Myc. Ven. no. 1060. Thom, The Penicillia, p. 561. 1930. Name was attached to a dried specimen but was not described.

P. glaucum var. *epixylon* de Thümen, in Myotheca universalis. Gallia. Cent. XIX, Wien. 1881. Thom, The Penicillia, p. 563. 1930. No description is given; this name should be dropped.

P. glaucum var. *fötidum* Sopp, in Monogr., pp. 141–143, Taf. XVI, fig. 110; Taf. XXII, figs. 1 and 2. 1912. Thom, The Penicillia, p. 561. 1930. Sopp's variety characterized by a strong odor and spores 5 by 5 or 6μ has not been identified with certainty.

P. glaucum var. *inodorum* Sopp, in Monogr., p. 143, Taf. XXII, fig. 3. 1912. Thom, The Penicillia, p. 562. 1930. Described as odorless and producing spores 7μ in diameter. Not identifiable.

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P. glaucum var. *pallidum* Sopp, in Monogr., p. 143, Taf. XVI, fig. 109. 1912. Thom, The Penicillia, p. 562. 1930. No one has been able to identify this.

P. gliocladioides Preuss, Fungi Hoyerswerda no. 16 in Linnaea **25:** 729. 1852. Thom, The Penicillia, p. 563. 1930. Not identifiable.

P. gliocladioides Spegazzini, in Myc. Arg. V. in Anales Mus. Nac. Buenos Aires, Ser. 3, T. **13:** 433. 1912. Sacc., Syll. **22:** 1277. 1913. Thom, The Penicillia, p. 563. 1930. The description presents bizarre features which render rediscovery improbable.

P. globosa (*Stysanus*) Peglion, 1895. In Biourge's Liste Onomastique, p. 103. 1923.

P. godlewskii Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 466–467; Taf. 45 and 49. 1927. Thom, The Penicillia, p. 365. 1930..... 312

P. gonorrhoicum Hallier, in Flora **51:** 294–300, fig. 9. 1868, is described as a penicillate form (Prap. nr. 342) assumed by *Cladosporium gonorrhoicum*. Thom, The Penicillia, p. 581. 1930. No description given and drawings inadequate for subsequent identification.

P. gorgonzola Weidemann, in Biourge, Monogr., La Cellule **33:** fasc. 1, pp. 204–206; Col. Pl. V and Pl. VIII, fig. 43. 1923. Thom, The Penicillia, pp. 284–285. 1930. A member of the *P. roqueforti* series doubtfully separable from the species, *P. roqueforti* Thom..... 400

P. gracile v.Szilvinyi in Zentbl. f. Bakt. etc. **103** (9/11): 152, 153, fig. 9. 1941. Without seeing the type, this appears to belong in the *P. janthinellum* series.

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P. grande, listed by Hallier in Flora **51:** 297. 1868; and in Zschr. f. Parasitenkunde I, 1868. Thom, The Penicillia, p. 563. 1930. Species never described.

P. granulatum Bainier, in Bul. Soc. Mycol. France **21:** 126–127; Pl. 11, figs. 2–7. 1905. Thom, The Penicillia, pp. 429–430, figs. 66 and 67. 1930..... 544

P. granulatum (?) Bainier, in Biourge Monogr., La Cellule **33:** fasc. 1, pp. 159–161; Col. Pl. II and Pl. III, fig. 17. 1923. See also Biourge, La Cellule **36:** 454. 1925. Thom, The Penicillia, pp. 430–431. 1930. Culture not received, probably some member of the *P. granulatum* series.

P. gratioti Sartory, in Ann. Mycol. **11:** 161–165, Pl. IX. 1913. Thom, The Penicillia, p. 338. 1930. Apparently some member of the *P. janthinellum* series.

P. griseo-atrum Biourge, in Monogr., La Cellule **33:** fasc. 1, p. 301; Col. Pl. XI and Pl. XIX, fig. 113. 1923. Thom, The Penicillia, p. 582. 1930.

Syn. *Aspergillus* of the *A. restrictus* series.

P. griseo-bruneum Sopp, in Monogr., pp. 153–155, Taf. XVII, fig. 117; Taf. XXII, fig. 6. 1912. Thom, The Penicillia, p. 286. 1930. Sopp described a strain, collected from a specimen of *Stereum*, with the general characters of the *P. roqueforti* series, but with all structures larger, especially conidia at 7.0 to 8.0μ in diameter. It has not since been reported.

P. griseo-brunneum Dierckx, in Soc. Scient. Bruxelles **25:** 88. 1901. Biourge, Monogr., La Cellule **33:** fasc. 1, pp. 162–163; Col. Pl. II and Pl. III, fig. 19. 1923. Believed to represent a synonym of *P. stoloniferum* Thom..... 413

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P. griseo-brunneum Sopp. Misspelling for *P. griseo-bruneum* Sopp. In Biourge's Liste Onomastique, p. 103. 1923.

P. griseo-fulvum Dierckx, in Soc. Scient. Brux. **25:** 88. 1901. In Biourge, Monogr., La Cellule **33:** fasc. 1, pp. 164–167; Col. Pl. II and Pl. II, fig. 11. 1923. Thom, The Penicillia, p. 371. 1930. Species regarded as belonging in *P. urticae series*..... 536

P. griseo-fulvum (Dierckx) Galeotti. In Biourge's Liste Onomastique, p. 103. 1923.

P. griseo-roseum Dierckx, in Soc. Scient. Bruxelles **25:** p. 89. 1901; Biourge, Monogr., La Cellule **33:** fasc. 1, pp. 168–170; Col. Pl. IV and Pl. VI, fig. 31. 1923; Thom, The Penicillia, pp. 263–264. 1930. Regarded as a synonym of *P. notatum* Westling..... 371

P. griseo-rubrum Dierckx. See Biourge, Monogr., La Cellule **33:** fasc. 1, Col. Pl. IV. 1923. Name represents a misprint for *P. griseo-roseum* Dierckx.

P. griseo-viride v.Szilvinyi in Zentbl. f. Bakt. etc. **103** (9/11): 170, fig. 23. 1941. The figure and description probably cover a variant of the *P. brevi-compactum* series.

P. griseum Bonorden, in Abh. Geb. Myk., p. 92. 1864. Thom, The Penicillia, p. 563. 1930. The species was never satisfactorily identified although this name has been used several times.

P. griseum Guegen. In Biourge's Liste Onomastique, p. 103. 1923.

Citromyces griseus Sopp, in Monogr., pp. 119–120, Taf. XV, fig. 104; Taf. XXII, fig. 5. 1912. Species not satisfactorily identified since described. A strain from CBS as *Citromyces griseus*

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Sopp, from Janke, approximates *P. restrictum* Gilman and Abbott—conidia are large and coarsely roughened in contrast to Sopp's "smooth." 225

P. griseus (*Citr.*) Sopp. In Biourge's Liste Onomastique, p. 103. 1923.

Scop. grylli Sartory, Sartory, and Meyer in Ann. Mycol. **30:** 466–470, 1 pl. 1930.

P. guegueni Biourge, in Biourge, Monogr., La Cellule **33:** fasc. 1, Liste Onomastique, p. 103, Col. Pl. XIII and Pl. XXII, fig. 128. 1923. Thom, The Penicillia, p. 583. 1930.

Syn. *Aspergillus gracilis* Bainier, from cultures received from Biourge.

P. guttulosum Gilman and Abbott, in Iowa State College, Jour Sci. **1:** 298, fig. 33. 1927. Thom, The Penicillia, p. 343. 1930. Regarded as a synonym of *P. janthinellum*; characterized by the production of excessive exudate 302

P. hagemi Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 448–450; Taf. 39. 1927. Thom, The Penicillia, pp. 298–299. 1930. Believed to represent a synonym of *P. brevi-compactum* Dierckx 411

P. hanzawanum Shih, in Trans. Sapporo Nat. Hist. Soc. XIV, Pt. 4, p. 291, Pl. XII, fig. 1. 1936. A biverticillate-symmetrical form in the *P. rugulosum* series approximating *P. tardum* Thom.

P. helicum Raper and Fennell, in Mycologia, **40:** 515–518, fig. 3. 1948 586

P. henebergi Drewes, in Milchw. Forsch. **18:** 289–330. 1937. This name was proposed but no description given for a *Penicillium* isolated from sour milk cheese, which was reported to

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differ somewhat from *P. camemberti*.

P. herquei Bainier and Sartory, in Bul. Soc. Mycol. France **28:** 121–126, Pl. VII. 1912; also Sartory and Bainier, Compt. Rend. Soc. Biol. Paris **71:** 229–230. 1911; Thom, The Penicillia, pp. 467–468, fig. 78. 1930 659

P. herquei Bainier and Sartory var. *lunzinense* v.Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 158. 1941. The data given are inadequate to justify recognition of the proposed variety.

P. hermanni v.Szilvinyi, in Zentbl. Bakt. etc. (II) **103:** 153, fig. 10. 1941. The describer placed his species in the Divaricata. No organism in this group has conidia globose, 5.0 to 5.5μ. His designation "floccose" would probably warrant placing it in the Lanata and regarding it as near to, if not identical with, *P. lanoso-viride* Thom. The type culture has not been seen.

P. heterocladum (*Vertic.*) Penzig. In Biourge's Liste Onomastique, p. 103. 1923.

P. (*Mieroaspergillus*) *hickeyi* Biourge in Monogr., La Cellule **33:** fasc. 1, pp. 103, 323, 328, Col. Pl. XIII and Pl. XXII, fig. 127. 1923. Thom, The Penicillia, p. 583. 1930. Culture examined by us. Synonym for *Aspergillus hickeyi* Biourge, assignable to the *A. restrictus* series.

P. hiemale (*Corcm.*) Bonorden, 1861. In Biourge's Liste Onomastique, p. 103. 1923.

P. hirsutum Bainier and Sartory, in Bul. Soc. Mycol. France **29:** 373–376. 1913. Thom, The Penicillia, p. 493. 1930. Species known only from description. Thom (1930, p. 493) regarded it as possibly approximating his *P. rolfsii*.

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P. hirsutum Dierckx, in Soc. Scientifique Bruxelles **25:** 89. 1901; Biourge, Monogr., La Cellule **33:** fasc. 1, pp. 157–159; Col. Pl. II and Pl. III, fig. 18. 1923. Thom, The Penicillia, pp. 425–426. 1930. Synonym of *P. corymbiferum* Westling 544

P. howardii Thom, in The Penicillia, p. 368. 1930. Species inadequately described. Now regarded as having represented a non-sclerotium-producing form approximating *P. raistrickii* Smith..... 277

P. huberi v.Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 159, fig. 13. 1941. Describer cited resemblances to *P. purpurogenum* (Fleroff) Stoll and to *P. rubrum* (Grassberger) Stoll but failed to show the distinctive characters of the Biverticillata-Symmetrica. Identity remains doubtful.

P. humicola Oudemans, in Arch. Neerlandaises der Sc. Exactes et Nat., p. 289, Tab. XXVI, fig. 1–5 1902. Thom, The Penicillia, p. 564. 1930. Identity questionable, probably some member of the Biverticillata-Symmetrica.

P. humuli van Beyma, in Zentbl. f. Bakt. etc. (II) **99:** 392–394, fig. 6. 1939..... 291

P. hyalina (*Glioceph.*) Matruchot, 1899. In Biourge's Liste Onomastique, p. 103. 1923.

P. hypo-janthinum Biourge, no. 25, in Monogr., La Cellule **33:** fasc. 1, p. 321–322; Col. Pl. XIII and Pl. XXII, fig. 130. 1923. Thom, The Penicillia, p. 583. 1930.

Syn. *Aspergillus hypojanthinus* Biourge, probably more correctly *A. gracilis* Bainier in *A. restrictus* series. Biourge's culture was examined by us.

P. hypomycetis Saccardo, in Sylloge **4:** 80. 1886.

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Syn. *Hypomyces aureo-nitens*, *fide* Plowright in Grevillea **11:** 49; Tab. 156, figs. e, d. 1882. Thom, The Penicillia, p. 584. 1930. Cultures from Grove's laboratory by Miss Elliott indicate that *Glioeladium roseum* was carried under this name.

P. implicatum Biourge, in Monogr., La Cellule **33:** fasc. 1, p. 278–280; Col. Pl. IX and Pl. XIV, fig. 82. 1923. Thom, The Penicillia, pp. 210–211. 1930..... 201

P. implicatum Biourge var. *aureo-marginatum* Thom, in The Penicillia, pp. 211–212. 1930. Regarded as having represented *P. multicolor* as considered in this Manual..... 201

P. incarnatum Berkeley and Broome, in Jour. Linn. Soc. Bot. **14:** 101. 1873; Sacc., Syll. **4:** 84. 1886. Thom, The Penicillia, p. 565. 1930. Species not identifiable.

P. ingelheimense van Beyma, in Antonie van Leeuwenhoek J. Microbiol. Serol. **8:** 109. 1942 599

Acaulium insectivorum Sopp, in Monogr., pp. 60–64, Taf. IV and VIII, figs. 66–69. 1912.

P. insectivorum (*Acaul.*) Sopp, 1912. In Biourge's Liste Onomastique, p. 103. 1923.

P. insigne Bainier, in Bul. Soc. Mycol. France **22:** 134, Pl. IX, figs. 5–12. 1906. Probable synonym of *P. albicans* Bainier..... 671

P. insolitum Morotchkovsky, in Bul. Sci. Rec. Biol. Univ. Kiev **2:** 77, fig. 6. 1936. A monoverticillate species possibly belonging to the *P. frequentans* series.

P. (*Citrom.*) *internascens* v.Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 148, fig. 6. 1941. Based upon the description and the type strain received from CBS this species is regarded as synonymous with *P. purpurrescens* (Sopp) n. comb..... 179

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P. internum Morotchkovsky (Bul. Sci. Rec. Biol. Univ. Kiev **2:** 78–79, fig. 8. 1936) is believed to represent a lightly colored form approximating *P. roseo-purpureum* Dierckx..... 220

P. intricatum Thom, in U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118; pp. 75–76, fig. 31. 1910; also, The Penicillia, p. 367. 1930. Regarded as probably approximating the type of culture now included in *P. godlewskii* Zaleski. 314

P. islandicum Sopp, in Monogr., pp. 161–164, Taf. XVII, fig. 122; Taf. XXIII, figs. 25 and 26. 1912. Thom, The Penicillia, pp. 466–467. 1930..... 623

P. italicum Wehmer, in Hedwigia **33:** 211–214. 1894; also Beitr. z. Kennt. Einh., Pilze II, 1, pp. 68–72; Taf. I, figs. 1–3, Taf. II, figs. 1–10, Jena, 1895. Thom, The Penicillia, pp. 412–414, fig. 63. 1930..... 526

Scop. ivorensis Boucher, in Bul. Soc. Path. Exot. **11:** 309–315. 1918.

P. janczewskii Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 488–490; Taf. 55. 1927. Thom, The Penicillia, p. 354. 1930. Synonym of *P. nigricans* (Bainier) Thom..... 329

P. janthinellum Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 258–260; Col. Pl. VII and Pl. XII, fig. 70. 1923. Thom, The Penicillia, pp. 338–341, fig. 52. 1930.. 299

P. jantho-citrinum Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 311–313, Col. Pl. IX and Pl. XV, fig. 90. 1923. Regarded as *P. terlikowskii* Zaleski..... 234

P. janthogenum Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 143–145; Col. Pl. II and Pl. III, fig. 13. 1923. Thom, The Penicillia, p. 387. 1930. Probably synonymous with *P. martensii* Biourge..... 503

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Carpenteles javanicum (van Beijma) Shear, in Mycologia **26:** 107. 1934..... 135

P. javanicum van Beijma, in Verhandel. Kon. Akad. Wetensch. Amsterdam Afd. Nat. (Tweede Sectie) **26** (4): 16–19, 3 figs. 1929; Lockwood *et al.*, Zentbl. f. Bakt. etc. (II) **90:** 412–413, fig. 1. 1934; Emmons, Mycologia, **27:** 145–146, figs. 12 and 16. 1935.. 135

P. jenseni Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 494–495; Taf. 57. 1927. Thom, The Penicillia, p. 346. 1930..... 322

P. johannioli Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 453–454; Taf. 40; 1927. Thom, The Penicillia, pp. 391–392. 1930. Believed to be synonymous with *P. martensii* Biourge..... 503

P. juglandis Weidemann, in Centbl. f. Bakt. etc. (II) **19:** 683–687, fig. 2. 1907. Thom, The Penicillia, p. 416. 1930. Synonym of *P. expansum* Link..... 516

P. kap-laboratorium Sopp, in Biourge, in La Cellule **36:** 454. 1925. Thom, The Penicillia, p. 407. 1930. Biourge regarded this as synonymous with his *P. leucopus* (Pers.) which we now regard as *P. expansum* Link.

P. kapuscinskii Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat Ser. B, pp. 484–485; Taf. 55. 1927. Thom, The Penicillia, p. 355. 1930..... 330

P. kiliense Weidemann, in Centbl. f. Bakt. etc. (II) **19:** 680–683, fig. 1. 1907; see Thom, The Penicillia, p. 455. 1930. Species not identifiable; relationship problematical.

Scop. koningii (Oud.) Vuill., in Bul. Soc. Mycol. France **27:** 143. 1911.

Syn. *Monilia koningi* Oud., in

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Arch. Neerland. Sc. Exact. et Nat., p. 23, Tab. XXI. 1902... 697

P. krzemieniewskii Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 490–492; Taf. 56. 1927. Thom, The Penicillia, p. 362. 1930. Regarded as a synonym of *P. daleae* Zaleski..... 298

P. kühnelti v.Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 154, fig. 11. 1941. Szilvinyi's meager figures suggest a member of the Biverticillata-Symmetrica as does also the excess of yellow hyphae reported.

Citromyces lacticus Mazé and Perrier, in Ann. Inst. Pasteur **18:** 558–559. 1904. Member of the *P. frequentans-spinulosum* complex, but closer diagnosis impossible..... 184

P. lacticus (Citr.) Mazé and Perrier, 1904. In Biourge's Liste Onomastique, p. 104. 1923.

P. lacticus Oertler (Birmingham). ?. In Biourge's Liste Onomastique, p. 104. 1923.

P. lagerheimi Westling, in Arkiv för Botanik **11:** 55, 110–112; figs. 25, 66a and b. 1911. Known only from description; Thom (1930, pp. 490–491) regarded it as probably an aberrant member of the Biverticillata-Symmetrica.

P. lagerheimii Westling, in Biourge, Monogr., La Cellule **33:** fasc. 1, p. 198, Col. Pl. III and Pl. V, fig. 30. 1923. Thom, The Penicillia, p. 491. 1930. Identity uncertain; doubtfully *P. lagerheimi* Westling.

P. (Citrom.) lanecolatum v.Szilvinyi in Zentbl. f. Bakt. etc. (II) **103:** 147, fig. 5. 1941. The describer put this species among the Monoverticillata but figured a penicillus with the lanceolate sterigmata of the Biverticillata-Symmetrica.

Scop. lanosa van Beyma, in Zentbl. f. Bakt. etc. (II) **96:** 423–425, fig. 1. 1937.

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P. lanoso-coeruleum Thom, in The Penicillia, pp. 322–323. 1930... 436

P. lanoso-griscllum Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 196–198; Col. Pl. III and Pl. V, fig. 25. 1923. Thom, The Penicillia, p. 246. 1930. Biourge's description suggests a possible variety of *P. digitatum* Sacc. or some form with nearly related morphology. The original culture was quickly lost and apparently not distributed.

P. lanoso-griseum Thom, in The Penicillia, p. 327. 1930..... 441

P. lanoso-viride Thom, in The Penicillia, pp. 314–315. 1930..... 434

P. lanoso-viride Thom var. *lunzininense* v.Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 162. 1941. Conidiophore walls reported as smooth, hence different from the species. Significance of character doubtful as warranting varietal status. Type culture not available.

P. lanosum Westling, in Arkiv för Botanik **11:** 55, 97–99, figs. 18 and 60. 1911. Thom, The Penicillia, pp. 317–318. 1930..... 431

P. lanosum Westling var. *lunzinense* v.Szilvinyi in Zentbl. Bakt. etc. (II) **103:** 165. 1941. The characters cited for this variety are regarded as strain variations not justifying separate description.

P. lapidosum Raper and Fennell, in Mycologia **40:** 524–527, fig. 6. 1948; Williams, Cameron, and Williams, Food Reseach **6:** 69–73. 1941..... 163

P. lavendulum Raper and Fennell, in Mycologia **40:** 530–533, fig. 8. 1948..... 464

P. lemoni Sopp, in Monogr., pp. 194–196; Taf. XX, fig. 152, Taf. XXIII, fig. 39. 1912. Thom, The Penicillia, pp. 469–470. 1930. Regarded as synonymous

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with *P. herquei* Bainier and Sartory 663

P. leucocephalum Rabenhorst, in D. C. Fl. n. 857.

Syn. *Rhodocephalus candidus* Corda in Icones Fungorum **I:** p. 2, fig. 282. 1837. Branching chains of conidia exclude this from *Penicillium*.

Coremium leucopus Persoon, in Myc. Europaea **1:** 42. 1822. Synonym of *P. expansum* Link.

P. leucopus (Pers.) Biourge, in Compt. Rend. Soc. Biol. Paris **82:** 877–880. 1919; also Monogr., La Cellule **33:** 107–111, Col. Pl. I and Pl. 1, fig. 1. 1923. Thom, The Penicillia, p. 408–409, fig. 62. 1930. Synonym of *P. expansum* Link 515

P. levitum Raper and Fennell, in Mycologia **40:** 511–515, fig. 2. 1948 148

P. lignicolum (*Gliocl.*) Matruchot, 1893. In Biourge's Liste Onomastique, p. 104. 1923.

Scop. lilacca Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 174. 1941.

P. lilacinum Thom, in U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118; pp. 73–75, fig. 30. 1910; also Thom, The Penicillia, pp. 331–334, figs. 49 and 50. 1930 285

P. "linguae (genre *Scopulariopsis)"*, Panayotatou, in Centbl. f. Bakt. etc. (I) **101:** 231–235; text figures 1–6. 1927. Thom, The Penicillia, p. 533. 1930. Isolated from a child's tongue in Alexandria, Egypt. Identified by Langeron as a *Scopulariopsis* 704

P. lividum Westling, in Arkiv för Botanik **11:** pp. 58, 134–137, fig. 79. 1911. Thom, The Penicillia, pp. 205–206. 1930 190

P. (*Citro.*) *lividum* Westling var. *lunzinense* v. Szilvinyi in Zentbl. f. Bakt. etc. (II) **103:** 147. 1941. Smooth, globose conidia exclude

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this mold from *P. lividum*. No type culture is available.

P. lobulatum Bon., in Abh. Geb. Myk., p. 92, 1864.

Syn. *Sporocybe lobulata* Berkeley. Thom, The Penicillia, p. 585. 1930. Distributed as *P. lobulatum* in Rabenhorst's Fungi Europaea no. 171. Black hyphae exclude it from *Penicillium*.

P. lunzinense v.Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 163–164, fig. 16. 1941. If the description correctly designates a floccose species, the other data given indicates a form closely related to *P. raciborskii* Zaleski.

P. luteo-viride Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 242–243, Col. Pl. VII and Pl. XI, fig. 62. 1923. Thom, The Penicillia, pp. 461–462, fig. 74. 1930. Based upon some member of the *P. funiculosum* series 620

P. luteo-viride Biourge var. *lunzinense* v.Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 158. 1941. The data given seem to ally this strain with the *P. rugulosum* series.

P. luteum Sopp, in Monogr., pp. 173–175; Taf. XXIII, fig. 23. 1912; see also, Thom, The Penicillia, p. 482. 1930. Not now identifiable; possibly synonymous with *P. sulfureum* Sopp.

P. luteum (?) Sopp, in Monogr., pp. 173–175; Taf. XXIII, fig. 23. 1912. Known only from description; possibly some member of the *P. purpurogenum* series.

P. luteum (Zukal?) Thom, in Biourge, Monogr., La Cellule **33:** fasc. 1, pp. 243–244; Col. Pl. XI and Pl. XVIII, fig. 103. 1923. Based on Biourge's culture No. 368 (Thom No. 11). Probably *P. vermiculatum* Dangeard 583

P. luteum Wehmer, in Biourge's Liste Onomastique, p. 104. 1923.

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P. luteum (Zukal) Wehmer, in Derx, in Bul. Soc. Mycol. France **41:** 375–381, 1925; also in Trans. Brit. Mycol. Soc. **11:** 108–112, Pls. I and II. 1926. Synonym of *P. luteum* Zukal; usage hinged upon Wehmer's publication (1893).

P. luteum Zukal, in Sitz.-Ber. Akad. Wien. **98:** 561. 1889. See also Wehmer, Ber. deut. Bot. Gesellsch. **2:** 499–516, Taf. 25. 1893; Emmons, Mycologia **27:** 141–143, figs. 10 and 16. 1935.. 600

P. luteum Zukal, in Thom, U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, 39–40. 1910. Culture underlying this usage subsequently shown to be *P. vermiculatum* Dangeard..... 583

P. luteum Zukal var. *lunzinense* v.Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 158. 1941. Smooth, globose conidia, 6.5 to 7.0μ in diameter, exclude this from the whole group to which *P. luteum* belongs. Without the type culture it is not identifiable.

Gymnoascus luteus (Zukal) Sacc., in Syll. **XI:** 437–438. 1895. Synonym of *P. luteum* Zukal, established upon bibliographic bases only.

P. macrosporum B. and Br., in Ann. and Mag. of Nat. Hist., Ser. 5, **9:** 183. 1882. Thom, The Penicillia, p. 565. 1930. Species not subsequently identified.

P. maculans Sharples, in Dept. Agr. Federated Malay States Bul. 19, p. 8. 1914. Thom, The Penicillia, p. 565. 1930. Regarded by this describer as the cause of spotting of plantation sheet-rubber. Species unidentifiable from the description.

P. majusculum Westling, in Arkiv för Bot. **11:** 51–52, 60–62, figs. 1 and 45. 1911. Thom, The Penicillia, pp. 389–390. 1930. Believed to be synonymous with *P. puberulum* Bainier..... 499

P. malivorum Cifferi, in Riv. Patol. Veget. **14:** 77–92. 1924. Thom, The Penicillia, pp. 409–410. 1930. Synonym of *P. expansum* Link..... 516

P. mandshuricum Saito, in South Manchuria Railway Company, Central Laboratory, Report No. 6, pp. 11–12. 1921. (In Japanese). Culture seen and assigned to *Paecilomyces* by Thom in The Penicillia, p. 550, 1930..... 689

P. mangini Duché and Heim, in Recueil de Travaux Cryptogamiques dédiés a Louis Mangin. Ext. pp. 20–24, fig. 4, Pl. 30, figs. 2–5. 1931. Apparently a member of the *P. thomii* series..... 165

P. martensii Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 152–154, Col. Pl. II and Pl. III, fig. 14. 1923. Thom, The Penicillia, pp. 388–389. 1930..... 500

P. martensii Biourge var. *lunzinense* v.Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 170. 1941. The description would put this in the series with *P. corymbiferum.*

P. matris-meae Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 477–479; Taf. 45 and 52. 1927. See Thom, The Penicillia, p. 349. 1930. Synonym of *P. soppi* Zaleski..... 282

P. maydis Lewin in Lehrbuch d. Toxicologie 2 aufl. Berlin, 1897. Cited by Lafar. Handb. d. Technischen Myk. 2 aufl. I, p. 613. Thom, The Penicillia, p. 565. 1930. Species not identifiable.

P. media (*Stysanus*) Sacc., 1881. In Biourge's Liste Onomastique, p. 104. 1923.

P. mediocre Stapp and Bortels, in Zentbl. f. Bakt. etc. (II) **93:** 50. 1935. Belongs with *P. spinu-*

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losum Thom but shows distinct strain characteristics 184

P. megalosporum Berkeley and Broome, in Ann. and Mag. of Nat. Hist., Ser. 4, **15:** 34. 1875. See Sacc. Sylloge **4:** 80. 1886. Thom, The Penicillia, p. 566. 1930. Species not identifiable.

P. megalosporum (*Gliocl.*) Marchal, 1895. In Biourge's Liste Onomastique, p. 104. 1923.

P. meleagrinum Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 147–149; Col. Pl. III and Pl. IV, fig. 22. 1923. Thom, The Penicillia, pp. 266–267. 1930 364

P. melinii Thom, in The Penicillia, p. 273. 1930 331

P. microsporum Rivolta, in Paras. Veget., p. 452. 1873. Thom, The Penicillia, p. 566. 1930. No data for identification.

P. miczynskii Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 482–484; Taf. 46, 53. 1927. Thom, The Penicillia, pp. 488–489. 1930 309

P. miczynskii Zaleski var. *lunzinense* v.Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 159. 1941. Without a type culture for examination the validity of this variety is doubtful.

P. minimum Siebenmann, in Zwitte vermehrte Ausgabe von Die Fadenpilze *Aspergillus* and *Eurotium*. Wiesbaden, pp. 82–83. 1889. Thom, The Penicillia, p. 566. 1930. Described only from material removed from a human ear membrane, on which it appeared as black spots. Conidiophores 20μ by 2μ; conidia globose, smooth, 2.5 to 3μ. Unexplained clumps of large brown cells. Not since reported, and probably unrecognizable.

Scop. minimus Sartory, Hufschmitt, and Meyer, in Bul. Acad. Med. Ser. 3, **103:** 604–606. 1930.

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P. minio-luteum Dierckx, in Soc. Scient. Bruxelles **25:** 97. 1901; also Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 237–239; Col. Pl. VII and Pl. XII, fig. 67. 1923; Thom, The Penicillia, p. 464. 1930. Regarded as synonymous with *P. funiculosum* Thom 621

P. minutum (*Citr.*) Sart.-Bain., in Biourge's Liste Onomastique, p. 104. 1923.

Citromyces minutus Bainier and Sartory, in Bul. Soc. Mycol. France **29:** 137–144, Pl. IV, fig. 3. 1913. Not recognized. Probably some representative of the Ramigena series 249

P. monilioïdes (*Isaria*) Albert Schw., 1805. In Biourge's Liste Onomastique, p. 104. 1923; the correct authority for this *Isaria* was Albertine and Schweinitz.

P. monstrosum Sopp, in Monogr., pp. 150–152, Taf. XVI, fig. 113; Taf. XXII, fig. 14. 1912. Thom, The Penicillia, p. 566. 1930. The descriptive data suggest contaminations. No one has since identified it.

P. montoyai Castellani and Chalmers, in Manual of Tropical Medicine, 1st Ed., 801. 1910. Thom, The Penicillia, p. 567. 1930. Data given is insufficient for identification.

P. morsus-ranae Corda, in Icones V, p. 53, Tab. II, fig. 23. 1842. Thom, The Penicillia, p. 567. 1930. Not surely identified since Corda.

P. mucosum Stapp and Bortels, in Zentbl. f. Bakt. etc. (II) **93:** 51. 1935. Regarded as *P. spinulosum* Thom but showing distinct strain characteristics 184

P. multicolor Grigorieva-Manoilova and Poradielova, in Arch. des

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Sciences Biologiques Leningrad **19:** 117–131, fig. 1 and one plate with photographs 1–6. 1915. (In Russian.) Thom, The Penicillia, pp. 212–213. 1930..... 198

P. multiforme v.Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 164–165, fig. 18. 1941. From the description, and without a type culture, this organism appears to approximate *P. aurantio-virens* Biourge.

Citromyces musae Bainier and Sartory, in Bul. Soc. Mycol. France **29:** 154–157; Pl. V, figs. 1–3. 1913. Not recognized. Probably some representative of the Ramigena series..... 249

P. musae Weidemann, in Centbl. f. Bakt. etc. (II) **19:** 687–689, fig. 3. 1907. Thom, The Penicillia, p. 393. 1930. Regarded as a synonym of *P. viridicatum* Westling. 486

P. mycetomagenum Mantelli and Negri, in Giorn. R. Acad. Med. Torino, Ser. IV, **21:** 165–166. 1915, as *P. mycetogenum* M. and N. Latin diagnosis by Negri, in Atti R. Accad. Sci. Torino **56:** 67–68. 1921, as *P. mycetomagenum* M. and N. Thom, The Penicillia, p. 567. 1930. Species identification impossible from the description; character of sclerotial masses suggests a member of the Biverticillata-Symmetrica.

P. mycetomi Neveu-Lemaire, in Précis de parasitologie humaine, 4th Ed., p. 123. 1908 (Paris). Thom, The Penicillia, p. 568. 1930. *Nomen nudum*, since species name cited without description.

P. nalgiovensis Laxa, in Zentbl. f. Bakt. etc. (II) **86:** 162–163. 1932..... 319

P. namyslowskii Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 479–480; Taf. 52. 1927. Thom, The Penicillia, pp. 484–485. 1930..... 462

P. necans (*Corem.*) Fischer, 1910. In Biourge's Liste Onomastique, p. 104. 1923.

P. necans (*Corem.*) Oudemans, 1903. In Biourge's Liste Onomastique, p. 104. 1923.

P. necrosiferum Morotchkovsky, in Bul. Sci. Rec. Biol. Univ. Kiev **2:** 79, fig. 9. 1936. Described in terms which seem to relate it to *P. citreo-viride* Biourge..... 218

Scop nieotianae van Beyma, in Zentbl. f. Bakt. etc. (II) **91:** 354–355, fig. 7. 1935.

P. nigrescens Junghuhn, in Batavia-asch Genootschape Verhandelingen V. 17. Praem. Flor. Crypt. Java. 1839.

Syn. *Coremium nigrescens* (Jungh.) Penz. Fungi Agron. No. 132, Sacc. Syll. **4:** 583; list in Syll. XI, p. 238. Thom, The Penicillia, p. 431. 1930. Known only from description. Probably some member of the *P. granulatum* series.

P. nigrescens (*Corem.*) Junghunder. In Biourge's Liste Onomastique, p. 104. 1923.

P. nigricans (Bainier) Thom, in The Penicillia, pp. 351–353, fig. 56. 1930..... 325

Glioeladium nigrovirens van Beyma, in Verh. Akad. Wet. Amst. (Tweede Sect.) **29:** 30–32, fig. 1. 1931.

P. nigrovirens Fresenius, in Beitr. z. Myk., p. 22, Taf. III, fig. 22. 1850. Thom, The Penicillia, p. 585. 1930.

Syn. Some *Cladosporium*.

Gliocladium nigro-virescens van Beyma, in Verh. Akad. Wetens. Amst. Natuurk. (Tweede Sect.) **29:** 30–32, fig. 1. 1931. This species is probably best assigned to the *G. deliquescens* series although it appears to be some-

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what transitional in the direction of *G. catenulatum* 687

Acaulium nigrum Sopp, in Monogr., pp. 47–53; Taf. X, figs. 86–89; Taf. XI, figs. 85, 92, 93; Taf. XII, figs. 90, 91. 1912. Apparently a *Scopulariopsis* with dark and very rough-walled conidia 701

P. niklewskii Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 504–505; Taf. 60. 1927. In *P. adametzi* series approximating that species 231

P. nivco-rubrum Sopp, in Monogr., pp. 190–192; Taf. XI, fig. 140; Taf. XVIII, figs. 139, 141; Taf. XX, fig. 142. 1912; see Thom, The Penicillia, p. 457. 1930. No one ventures an identification of this species.

P. niveum Bainier, in Bul. Soc. Mycol. France **22:** 134, Pl. IX, figs. 1–4. 1906.

Probably synonym of *P. albicans* Bainier 671

P. niveum Sopp, in Monogr., pp. 182–184, Taf. XXIII, fig. 16. 1912. Thom, The Penicillia, p. 242. 1930. Description based upon a white colony with penicillate conidial structures and abundant conidia 9.0 by 18 to 20μ. Possible relationship to *P. digitatum* Sacc. var. *californicum* Thom is suggested 390

P. niveum (*Corem.*) Corda, 1838. In Biourge's Liste Onomastique, p. 104. 1923.

P. notatum Westling, in Arkiv för Botanik **11:** 55, 95–97; figs. 17 and 59. 1911; Biourge, Monogr., La Cellule **33:** fasc. 1, pp. 179–181; Col. Pl. IV and Pl. VIII, fig. 37. 1923; Thom, The Penicillia, pp. 264–265. 1930. . . . 367

P. novae-zeelandiae van Beyma, in Antonie van Leeuwenhoek **6:** 273–275, fig. 7. 1939–1940. Assignable near *P. herquei* Bain. in the Biverticillata-Symmetrica 665

P. obscurum Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 267–269; Col. Pl. VIII and Pl. XIV, fig. 80. 1923. Thom, The Penicillia, p. 251. 1930. Regarded as a synonym of *P. corylophilum* Dierckx 344

P. ochracea (*Oospora*) (Libert) Sydow, 1921. In Biourge's Liste Onomastique, p. 104. 1923.

P. ochracea (*Spicar.*) (Bouldier) Vuillem. In Biourge's Liste Onomastique, p. 104. 1923.

P. ochraceum Raillo, in Zentbl. f. Bakt. etc. (II) **78:** 522. 1929. Apparently a member of the *P. implicatum* series.

P. ochraceum (Bainier) Thom, in The Penicillia, p. 309. 1930. . . . 477

P. ochraceum var. *macrosporum* Thom, in The Penicillia, p. 310. 1930. A large-spored variant of *P. ochraceum* (Bain.) Thom. Variety no longer recognized . 479

P. ochro-chloron Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 269–270; Col. Pl. X and Pl. XVII, fig. 100. 1923. Thom, The Penicillia, p. 363. 1930. . . . 305

P. ochroleucum Artault, in Recherches bacteriologiques, mycologiques, zoologiques et medicales sur l'oeuf de poule, pp. 213–214. 1893. Thom, The Penicillia, p. 568. 1930. Species not identifiable.

P. oidiforme Orlova, in Jour. Soc. Bot. Russia **10:** 375–394, 8 figs. 1925. (In Russian with French résumé.) Thom, The Penicillia, p. 585. 1930. Not a *Penicillium*.

Scop. oidiospora Zach, in Osterr. Bot. Zeitsch. **83:** 182–184, figs. 7 and 8. 1934.

P. olcdzkii Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 499–501; Taf. 59.

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1927. Regarded as a synonym of *P. frequentans* Westling..... 177

Scop. olivacea Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 174, fig. 28. 1941.

Scop. olivacea var. *parva* Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 174. 1941.

P. olivaceum Corda, in Icones **3:** 12, Taf. II, fig. 35. 1839. Thom, The Penicillia, p. 586. 1930.

Syn. Some *Cladosporium*.

P. olivaceum (?) Sopp, in Monogr., pp. 176–179, Taf. XIX, fig. 133, 135, and Taf. XXIII, fig. 29, 30. 1912. Thom, The Penicillia, p. 246. 1930. Probably *P. digitatum* Saccardo, and apparently derived directly from Wehmer's strain of *P. olivaceum* Wehmer.

P. olivaceum Wehmer, in Beitr. z. Kenntn. Einh., Pilze II, 1, pp. 73–76; Taf. I, fig. 2, Taf. II, figs. 11–15; Jena. 1895. Thom, The Penicillia, p. 245. 1930. Synonym of *P. digitatum* Saccardo. 390

P. olivaceum var. *discoidcum* El. and Em. Marchal, in Bul. Soc. Roy. Bot. Belg. **54:** 129. 1921. Thom, The Penicillia, p. 586 (also p. 246). 1930. Description suggests some species of *Metarrhizium*.

P. olivaceum Sopp (?) var. *italicum* Sopp, in Monogr., p. 179, Taf. XIX, fig. 133; Taf. XXIII, fig. 29. 1912. Varietal designation based upon a culture isolated from an orange of Italian origin and showing conidia smaller than in var. *norvegicum*. Wehmer's prior use of *P. olivaceum* is not cited. Synonym of *P. digitatum* Sacc.

P. olivaceum Sopp (?) var. *norvegicum* Sopp, in Monogr., pp. 177–179, Taf. XIX, fig. 135; Taf. XXIII, fig. 30. 1912. Varietal designation based upon Norwegian origin of strain and large, variable conidia. Wehmer's prior use of the binomial *P. olivaceum* is not mentioned. Probable synonym of *P. digitatum* Sacc.

Citromyces olivaceus Sopp, in Monogr., pp. 129–131; Taf. XIV, fig. 99; Taf. XXII, fig. 11. 1912. A strictly monoverticillate *Penicillium* with spores globose and smooth, 6 by 5μ and dark colored in mass, probably belongs with *P. purpurrescens* as accepted here, but conidia not reported as rough.

P. olivaceus (*Citr.*) Sopp. Cited in Biourge's Liste Onomastique, p. 104. 1923.

P. olivino-viride Biourge, in Monogr., La Cellule **33:** fase. 1, pp. 132–133; Col. Pl. II and Pl. II, fig. 12. 1923. Thom, The Penicillia, pp. 393–394. 1930..... 487

P. olsoni Bainier and Sartory, in Ann. Mycol. **10:** 398–399; Pl. VI, figs. 1–8. 1912. Thom, The Penicillia, pp. 471–472. 1930.... 664

P. ophioglossoides (*Isaria*) de Stephani, 1912. In Biourge's Liste Onomastique, p. 104. 1923.

P. opoixi (*Oospora*) Delacroix, 1897. In Biourge's Liste Onomastique, p. 104. 1923.

P. orbicula Corda, in Icones **3:** 12, Taf. II, fig. 34. 1839. Thom, The Penicillia, p. 586. 1930.

Syn. *Briarea orbicula* (Corda) Bon. in Saccardo Syll. **IV:** 85. 1886.

P. orbicula (*Briarea*) Corda, 1839. In Biourge's Liste Onomastique, p. 104. 1923.

Scop. oudemansii Vuill., in Bul. Soc. Mycol. France **27:** 143. 1911. Identity of strain studied is not known.

P. ovoideum Preuss, Fungi in Linnaea **26:** 708. 1853. Thom, The Penicillia, p. 586, 1930. Species not identifiable.

P. oxalicum Currie and Thom, in

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Jour. Biol. Chem. **22** (2): 289, fig. 1. 1915. Thom, The Penicillia, pp. 247–248. 1930. 378

Citromyces oxalicus Mazé and Perrier, in Ann. Inst. Pasteur **18:** 558–559. 1904. A member of the *P. frequentans-spinulosum* complex, but closer diagnosis impossible 184

P. paczoskii Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 505–507; Taf. 47, 61. 1927. In the *P. adametzi* series approximating *P. terlikowskii* Zaleski 233

P. paeciliforme v.Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 156, fig. 12. 1941. Regarded by van Beyma and by us as synonymous with *P. camemberti*.

P. palitans Westling, in Arkiv för Botanik **11:** 53, 83–86, figs. 54 and 12. 1911. Thom, The Penicillia, pp. 396–397. 1930.... 488

P. pallidofulvum Peck, in New York State Museum Bul. 67, p. 30. 1903. Thom, The Penicillia, p. 568. 1930. The specimen was lost, hence is not identifiable.

P. pallidum Smith, in Brit. Mycol. Soc. Trans. **18:** 88, Pl. IV; figs. 1 and 2. 1933. 461

P. parasiticum Sopp, in Monogr., pp. 164–166, Taf. XII, fig. 127; Taf. XVIII, fig. 129; Taf. XXIII, fig. 19. 1912; see Thom, The Penicillia, p. 455. 1930. Species unidentifiable; not subsequently reported. Possibly a member of the *P. luteum* series.

P. parvum Raper and Fennell, in Mycologia **40:** 508–511, fig. 1. 1948. 138

P. patris-mei Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 496–498; Taf. 58. 1927. Thom, The Penicillia, p. 303. 1930. Believed to represent a synonym of *P. brevicompactum* Dierckx 411

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P. patulum Bainier, in Bul. Soc. Mycol. France **22:** 208, Pl. XI, figs. 14–17. 1906; also *ibid.* **23:** Pl. V, figs. 10–16. 1907. Thom, The Penicillia, p. 420. 1930. Regarded as synonymous with *P. urticae* Bainier..... 534

P. pavoninum v.Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 165, fig. 19. 1941. Regarded as approximating *P. palitans*.

P. paxilli Bainier, in Bul. Soc. Mycol. France **23:** 95–96; Pl. X, figs. 1–4. 1907. Thom, The Penicillia, pp. 294–295. 1930..... 414

Mucor penicillatus Bulliard, in Herbier de la France, Vol. **3:** Pl. 504, fig. XI. 1791 (in U. S. Dept. Agr. Library); Histoire des champignons de la France tome 1, partie 1, Paris. 1809. (in Farlow Library). The figures given place the material in *Penicillium* but do not permit of species identification..... 3

P. penicillioides (Delacr.) Vuillemin. Bul. Soc. Mycol. France **27:** 75–76. 1911.

Syn: *Monilia penicillioides* Delacroix. Bul. Soc. Mycol. France **13:** 114–115, Pl. IX. 1897.

Scop. penicillioides (Delacr.) Smith and Ramsbottom, in Brit. Mycol. Soc. Trans. **5:** 164. 1915. Some *Scopulariopsis* is involved.

Gliocladium penicilloides Corda, in Icones Fungorum **IV:** 30–31, Taf. VII, fig. 92. 1840. Cited as *P. penicillioides* (Gliocl.) Corda-Matruchot, 1895; in Biourge's Liste Onomastique, p. 105. 1923..... 679

P. persimplex Klebahn, in Ber. Deut. Bot. Gesell. **51:** 318–323, fig. 1. 1933. Doubtfully a *Penicillium* from description and figures. Culture received from Baarn as Klebahn's type failed to produce conidia.

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P. pertardum Biourge, in Monogr., La Cellule **33:** fasc. 1, Col. Pl. XIII and Pl. XXII; fig. 132. 1923. Thom, The Penicillia, p. 587. 1930.

Syn: *Aspergillus pertardus* Biourge; culture as distributed was one of the *A. restrictus* series.

P. petchii Sartory and Bainier, in Ann. Mycol. **11:** 272–277, Pl. XIV, figs. 1–12. 1913: see Thom, The Penicillia, p. 454, fig. 71. 1930. Species not identifiable from description, but figures and colors reported indicate some member of the *P. luteum* group.

P. pezizoides Biourge, name proposed in La Cellule **36:** 453–454. 1925; cited by Thom in The Penicillia, p. 568. 1930, but no description given. Biourge's culture (subsequently received) is regarded as doubtfully separable from *P. puberulum* Bainier 500

P. pfefferianum series, in Thom's The Penicillia, pp. 182–183. 1930. Forms contained therein are included in *P. spinulosum* Thom 172

P. pfefferianum (Wehmer) Pollacci, in Atti Ist. Bot. Univ., Pavia, Ser. II, **16:** 121–136, Pl. XVI. 1916. Probably belongs in *P. frequentans* Westling 177

P. pfefferianum (Wehmer) Westling, in Arkiv för Botanik **11:** 132–133. 1911. Regarded as *P. spinulosum* Thom 184

P. pfefferianum (Citr.) Wehmer. In Biourge's Liste Onomastique, p. 105. 1923.

Citromyces pfefferianus Wehmer, in Beitr. z. Kenntn. einheim. Pilze **I:** 22–24; Taf. I, figs. 1–13. 1893; also Saccardo Sylloge Fungorum **XI:** 593. 1895. Believed to have represented a form approximating *P. spinulosum* Thom 184

P. phaco-janthinellum Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 289–290; Col. Pl. VIII and Pl. XIII, fig. 77. 1923. Regarded as approximating *P. fellutanum* Biourge 214

P. phoeniceum van Beyma, in Zentbl. f. Bakt. etc. (II) **88:** 136–317, figs. 4 and 5. 1933 236

P. piceum Raper and Fennell, in Mycologia **40:** 533–535, fig. 9. 1948 627

P. pictor Neveu-Lemaire, in Précis Parasitol. 1908. (Paris). Recited in *idem.* 5th Ed., p. 89. 1921. (Paris). Regarded as synonym of *P. montoyai* Castellani and Chalmers by these authors in Manual Tropical Medicine, 1st Ed., p. 801. 1910. Data presented in neither case is adequate for identification.

P. pigmentaceum Raillo, in Zentbl. f. Bakt. etc. (II) **78:** 522. 1929. Apparently a member of the *P. implicatum* series.

P. pinophilum Hedgcock in Thom, U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, pp. 37–38, fig. 6. 1910; also Thom, The Penicillia, p. 462., figs. 75 and 76. 1930. Erroneously discussed as *P. aureum* Corda by Hedgcock in Mo. Bot. Gard. Rpt. 17, pp. 105–107, pl. II, figs. 1–3. 1906. Regarded as synonymous with *P. funiculosum* Thom 620

P. piscarium Westling, in Arkiv för Botanik **11:** 54, 86–88, figs. 13 and 55. 1911. Thom, The Penicillia, pp. 487–488. 1930 308

P. platense Spegazzini, in Rev. Agr. y. Veter. La Plata (1896), p. 246. Thom, The Penicillia, pp. 196–197. 1930. A monoverticillate form described from lesions on sugarcane. Not known in culture. Assignment questionable.

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Fascicles or ropes of hyphae bearing conidial structures suggests *P. adametzi* series as a possibility.

P. plicatum Bon., in Hanb., p. 75, fig. 81. 1851. Thom, The Penicillia, p. 569. 1930. No satisfactory basis for identification is given.

P. plumiferum Demelius, in Verhandl. Zool.-Bot. Gessellsch. Wien. **72:** 76, fig. 5. (1922) 1923. Thom, The Penicillia, p. 410. 1930. Synonym of *P. expansum* Link..... 516

P. poiraulti Raciborski, in Flora **82:** 119–120. 1896. Thom, The Penicillia, p. 569. 1930. *Nomen nudum.*

P. polonicum Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 445–447, Taf. 38. 1927. Thom, The Penicillia, p. 421. 1930. In the *P. cyclopium* series nearest *P. martensii* Biourge..... 503

P. polyactis Secretan, in Mycographie Suisse **111:** 537. 1833. Thom, The Penicillia, p. 587. 1930. Not a *Penicillium.*

Scop. polychromica Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 175, fig. 29. 1941.

P. populi van Beyma, in Zentbl. f. Bakt. etc. (II) **96:** 419–421, fig. 1. 1937. A funiculose species regarded as probably close to *P. terrestre* Jensen.

P. porraceum Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 188–189; Col. Pl. V and Pl. IX, fig. 49. 1923. Thom, The Penicillia, p. 401. 1930. Regarded as a synonym of *P. puberulum* Bainier..... 500

P. proliferum (*Gliocl.*) Matruchot, 1893. In Biourge's Liste Onomastique, p. 105. 1923.

P. proprium Morotchkovsky (Bul. Sci. Recueil Biol. Univ. Kiev. **2:** 78, fig. 7. 1936) is believed to represent some member of the *P. janthinellum* series..... 303

P. pruriosum Salisbury (1873), cited in Marchand, Bot. Crypto-Pharm., p. 194, fig. 45a–d, 1883. Thom, The Penicillia, p. 569. 1930. Species not identifiable.

P. psichydae (*Spic.*) (Evans, 1912). In Biourge's Liste Onomastique, p. 105. 1923.

P. psittacinum Thom, in The Penicillia, p. 369. 1930..... 448

P. puberulum Bainier, in Bul. Soc. Mycol. France **23:** 16–17; Pl. IV, figs. 6–12. 1907. Thom, The Penicillia, pp. 271–273, figs. 36 and 37. 1930..... 497

P. pulvillorum Turfitt, in Brit. Mycol. Soc. Trans. **23:** 186–187, Pl. IV. 1939. A sclerotium-forming species in the *P. raistrickii* series..... 277

P. purpurascens (*Citr.*) Sopp. Misprint for *P. purpurrescens* Sopp in Biourge's Liste Onomastique, p. 105. 1923.

P. purpurogenum Fleroff-Stoll, in Biourge Monogr., La Cellule **33:** fasc. 1, pp. 235–237; Col. Pl. VII and Pl. XI, fig. 66. 1923. Thom, The Penicillia, pp. 478–479. 1930. Regarded as synonymous with *P. purpurogenum* Stoll..... 636

P. purpurogenum Stoll, in Beitr. z. Morph. u. biol. Char. Penicill. Wurzburg, p. 32, t. I, fig. 6, t. III, fig. 2. 1904. Also Thom, U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, p. 36, fig. 5. 1910; and Mycologia **7:** 134–142. 1915. Thom, The Penicillia, p. 478. 1930..... 633

P. purpurogenum Stoll var. *rubrisclerotium* Thom, in Mycologia **7:** 141–142, fig. 1. 1915. Thom, The Penicillia, p. 479. 1930..... 636

P. purpurrescens (Sopp) n. comb... 177
Syn. *Citromyces purpurrescens*

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Sopp, in Monogr., pp. 117–119. Taf. XIV, fig. 102; Taf. XXII, fig. 4. 1912.

P. pusillum Smith, in Brit. Mycol. Soc. Trans. **22:** 254–255, Pl. XVI, figs. 7–8. 1939..... 167

P. putterillii Thom, in The Penicillia, p. 368. 1930..... 461

P. quadrifidum Salisbury, in Zeitschr. Parasitenkunde **4:** 1–5, Taf. 1, fig. 1, a–e. 1875. Thom, The Penicillia, p. 569. 1930. Species not identifiable.

Monilia racemosa Pers., Syn. Meth. Fung., p. 692, and based upon Micheli Pl. 91, fig. 4. Thom, The Penicillia, p. 587. 1930. Cited as a *Penicillium* by Hoffman from Westendorp's Herb. Crypt. No. 196. Not determinable if a *Penicillium*.

P. raciborskii Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B., pp. 454–455, Taf. 36. 1927; also Thom, The Penicillia, pp. 318–319. 1930..... 333

P. raciborskii Zaleski var. *lunzinense* v.Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 165. 1941. This is believed to represent some member of the *P. terrestre* series although the type strain has not been available for observation.

P. radians Bonorden, in Abh. a. d. Geb. Myk. p. 92, 1864. Thom, The Penicillia, p. 570. 1930. Species not identifiable.

P. radiatum Lindner, in Mikrosc. Betriebskontr., p. 314. 1901; also *ibid.*, 5 aufl. pp. 383–384, fig. 164. 1909. Thom, The Penicillia, p. 587. 1930. The original material contained two molds, one a monoverticillate *Penicillium* which is not identifiable (seen by C .T.); the other represented some other genus.

P. raistrickii Smith, in Brit. Myc. Soc. Trans. **18:** 90, Pl. IV, fig. 4; Pl. V, figs. 5 and 6. 1933..... 275

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P. ramifer (*Stysanus*) Rolland, 1890. In Biourge's Liste Onomastique, p. 105. 1923.

Citromyces ramosus Bainier and Sartory, in Bul. Soc. Mycol. France **29:** 144–148, Pl. IV, figs. 1 and 2. 1913. Figures indicate some ramigenous form. Not identified..... 249

P. ramosus (*Citr.*) Sopp. In Biourge's Liste Onomastique, p. 105. 1923.

P. repandum Bainier and Sartory, in Bul. Soc. Mycol. France **29:** 367. 1913. Thom, The Penicillia, p. 550. 1930. The description suggests some *Paecilomyces*..... 689

P. repens Cooke and Ellis, in Grevillea **7:** 6. 1878: type no. 553 in North American Fungi, Newfield, N. J. October, 1879. Thom, The Penicillia, p. 587, fig. 99. 1930.

Syn. *Haplographium delicatum* B. and Br. *fide*. E. W. Mason in annotated account of the fungi received at the Imperial Inst. List 2, fasc. 2, pp. 62–63. 1933.

P. (*Scop.*) *repens* (Bain.) Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 225–226; Col. Pl. XII, Cart. 362, Pl. XX, fig. 119. 1923. Biourge's rearrangement of Bainier's usage.

Scop. repens Bainier, in Bul. Soc. Mycol. France **23:** 125–127, Pl. XVI, figs. 1 and 2. 1907.

P. resticulosum Birkinshaw, Raistrick, and Smith, in Biochem. Jour. **36:** 829–835. 1942..... 455

P. restrictum Gilman and Abbott, in Iowa State College Jour. Sci. **1:** 297, fig. 32. 1927. Thom, The Penicillia, pp. 176–177, fig. 20. 1930..... 223

P. rivolii Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 471–473; Taf. 50. 1927. Thom, The Penicillia,

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p. 342. 1930. Regarded as a synonym of *P. janthinellum* Biourge..... 303

P. (*Citrom.*) *rivolii* Zaleski var. *lunzinense* v.Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 148. 1941. There seems to be little reason for separating the variety from the species which we consider to be synonymous with *P. janthinellum.*

Citromyces robustus Sopp, in Monogr., pp. 125–126, Taf. XV, fig. 103; Taf. XXII, fig. 8. 1912. Believed to have represented some member of the *P. frequentans* series.

P. rogeri Wehmer, in Lafar Hdb. Tech. Mycol. 2 aufl. **4:** 226. 1906. Synonym of *P. easeicolum* Bainier..... 422

P. rolfsii Thom, No. "32", in U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118: pp. 80-81, fig. 36. 1910. Thom, The Penicillia, pp. 489–490, fig. 86. 1930..... 282

P. roquefort Sopp, in Monogr., pp. 156–157, Taf. XVII, figs. 118–119; Taf. XXII, figs. 7–8. 1912. Thom, The Penicillia, pp. 285–286. 1930. A synonym of *P. roqueforti* Thom..... 399

P. roqueforti Thom, in U. S. Dept. Agr., Bur. Anim. Ind., Bul. 82, pp. 35–36, fig. 2. 1906. See also *ibid.*, Bul. 118, p. 34, fig. 4. 1910; and The Penicillia, pp. 277–279, fig. 38. 1930..... 395

P. roqueforti var. *megalospora* (MS. variety of Dierckx), in Biourge's Monogr., La Cellule **33:** fasc. 1, p. 203. 1923. Thom, The Penicillia, p. 281. 1930. Name applied to a member of *P. roqueforti* series with conidia 5.5 by 4.5μ, occasionally 7.2 by 6.5μ in terminal cells. Such strains have been seen but are not sufficiently unique to warrant separate nomenclature.

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P. roqueforti var. *viride* Dattilo-Rubbo, in Brit. Mycol. Soc., Trans. **22:** 174–181. 1938. Synonym of *P. roqueforti* Thom.... 398

P. roqueforti Thom var. *weidemanni* Westling, in Arkiv för Bot. **11:** 52, 71–73, figs. 6 and 49. 1911; cited by Biourge, Monogr. p. 204, 1923, as *P. weidemanni* Westling. Thom, The Penicillia, p. 281. 1930. Synonym of *P. roqueforti* Thom..... 399

Scop. rosacea Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 175, fig. 30. 1941.

P. rosato-fragrans Biourge, in Monogr., La Cellule **33:** fasc. 1, p. 225; Col. Pl. VI and Pl. X, fig. 60. 1923. Thom, The Penicillia, p. 570. 1930. *Nomen nudum.*

P. (*Oospora*) *rosatum* Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 228–229; Col. Pl. XII, Cart. 393; Pl. XXI, fig. 123. 1923. Regarded by Biourge as a *Penicillium*—probably represents a *Scopulariopsis.*

P. roseo-cinnabarinum Biourge, in Monogr., La Cellule **33:** fasc. 11, pp. 319–321; Col. Pl. X and Pl. XVII, fig. 97. 1923. A monoverticillate form believed to have approximated *P. implicatum* Biourge.

P. roseo-citreum Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 184–186; Col. Pl. IV and Pl. VII, fig. 39. 1923. Thom, The Penicillia, pp. 323–324. 1930. Regarded as a synonym of *P. chrysogenum* Thom; species apparently based upon an unusually floccose strain..... 364

P. roseo-griseum, in Biourge's Monogr., La Cellule **33:** 171. 1923. Probably a misprint for *P. griseo-roseum* Dierckx.

P. roseo-maculatum Biourge, in Monogr., La Cellule **33:** fasc. 1,

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pp. 301–303; Col. Pl. VIII and Pl. XII, fig. 71. 1923. Regarded as *P. spinulosum* Thom. 185

P. rosco-purpureum Dierckx, in Soc. Scientifique Bruxelles **25:** p. 86. 1901. In Biourge, Monogr., La Cellule **33:** fasc. 1, pp. 317–319; Col. Pl. X and Pl. XVI, fig. 96. 1923; *ibid.* **36:** 482. 1925. Thom, The Penicillia, p. 181. 1930 218

P. roseo-viridum Stapp and Bortels, in Zentbl. f. Bakt. etc. (II) **93:** 51. 1935. Description and type culture indicate that this is synonymous with *P. aurantio-violaceum* Biourge 194

P. roseum Link, in "Obs." II, p. 37. 1816; see also Link, Sp. Plant Ed. 4, Vol. 6, pt. 1, p. 69, 1824; Fries Sys. Myk. 3, p. 409, 1829; Pers. Myc. Europ., 1822.

Syn. *G. roseum* (Link) Bainier 678

P. roseum (de Kral) Thom, 1910. In Biourge's Liste Onomastique, p. 105. 1923.

P. roseum (*Gliocl.*) Matruchot, 1893; Bain., 1907. In Biourge's Liste Onomastique, p. 105. 1923.

P. roseum (*Vertic.*) Cooke, in Syll., 1886. In Biourge's Liste Onomastique, p. 105. 1923.

P. roseum var. *coremioides* Kiekx, in Saccardo Sylloge **IV:** 83. 1886. Certainly one of the *G. roseum* series.

Acrostolagmus roseus Bainier, in Bul. Soc. Mycol. France **21:** 225–227, Pl. 12, figs. 1 to 9. 1905. Regarded as possibly representing *Gliocladium roseum* (Link) Bainier 680

P. rotundum Raper and Fennell, in Mycologia **40:** 518–521, fig. 4 591

P. (*Scop.*) *rubellum* (*Bainier*) Biourge. See *P. amethystinum* above. Synonym of *P. lilacinum* Thom 288

Scop. rubellus Bainier, in Bul. Soc. Mycol. France **23:** 104, Pl. XII, figs. 6–11. 1907. Not *S. rubellus* Bainier of Biourge's Monograph.

P. rubens Biourge, in Monogr., La Cellule **33:** fasc. 1, p. 265; Col. Pl. XI and Pl. XIX, fig. 111. 1923. Thom, The Penicillia, p. 249, fig. 33. 1930. Culture received as type represents a form approximating *P. chrysogenum* Thom 364

Citromyces rubescens Sopp, in Monogr., pp. 126–128; Taf. XIII, fig. 97; Taf. XXII, fig. 9. 1912. Monoverticillate form of uncertain relationship. Possibly approximating *P. roseo-purpureum* Dierckx.

P. rubescens (*Citro.*) Sopp. In Biourge's Liste Onomastique, p. 105. 1923.

P. rubescens Bainier, in Bul. Soc. Mycol. France **22:** 207, Pl. XI, figs. 7–13. 1906 671

P. rubro-punctatum Dierckx, in Soc. Sci. Brux. **25:** 85. 1901. Thom, The Penicillia, p. 570. 1930. No one has ever identified Dierckx's species.

P. rubrum, see fig. 131 in Sopp, Monogr. Taf. XVIII, fig. 131, also p. 164. 1912. This organism was figured and named by Sopp in his table XVIII, then discussed by name and discarded without decision, as to its allocation. It was listed as a yellow organism which produced perithecia. The penicillus figured might represent some variant member of the *P. luteum* series. The name was untenable in any case.

P. rubrum (?) Grassberger-Stoll, in Biourge, Monogr , La Cellule **33:** fasc 1, pp. 172–174; Col. Pl. IV and VI, fig. 33. 1923. Thom (1930, p. 250) assigned this species to *P. rubens* Biourge upon the basis of a culture sup-

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plied by Biourge under the above name.

P. rubrum Sopp, in Videnskapselskapets Skr. I. Mat.-Naturv. Kl. Kristiania 1911, no. 2, pp. 19–20, Taf. 5, figs. 28–29. 1912. Also fig. 131, Taf. XVIII in same Skr. No. 11, 1912. Thom, The Penicillia, p. 570. 1930. Sopp describes one of the sclerotium forming monoverticillate group near *P. thomii* Maire but has given no means for closer identification.

P. rubrum Stoll, in Beitr. z. morph. u. biol. Char. *Penicillium* Wurzburg, p. 35, Taf. I, fig. 7, Taf. III, fig. 3, Taf. IV, fig. 4. 1904. Also Thom, U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, p. 39, fig. 7. 1910; and Thom, The Penicillia, p. 476. 1930. 637

P. rufescens Bainier. In Biourge's Liste Onomastique, p. 105. 1923. Probably a misprint for *P. rubescens* Bainier.

P. rufescens Biourge, in Monogr., La Cellule **33:** fasc. 1, Col. Pl. XI. 1923. Apparently an incorrect citation of *P. rubens* Biourge.

Scop. rufulus Bainier, in Bul. Soc. Mycol. France **23:** 105, Pl. XII, figs. 1–5. 1907. Biourge suggested *P.* (*Scop.*) *rufulum* (Bainier) Biourge as a name change and suggested synonymy with *Torula rufescens* Fresenius.

P. rugulosum Thom, in U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, pp. 60-61, fig. 21. 1910. Thom, The Penicillia, pp. 472–473. 1930. 648

P. rugulosum var. *atricolum* (Bainier?) Thom, n. var., in The Penicillia, p. 474. 1930. Recognition of the variety no longer considered warranted. . . 653

P. rugulosum Thom var. *lunzinense* v.Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 160. 1941. The descriptive notes exclude this from *P. rugulosum* but do not furnish enough data for determination.

P. ruttneri v.Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 160–161, fig. 14. 1941. The describer put this species in Biverticillata-Symmetrica, but no such diminutive form has been recorded by any other author. Unless refound and more completely described, species should be dropped.

P. sacchari Ray, in Rev. Gen. Bot. **9:** 294–300; Pl. 16, figs. 23–27. 1897; see Thom, The Penicillia, p. 452. 1930. An ascosporic member of the *P. luteum* series; not reported since described. Possibly approximates *P. helicum* Raper and Fennell 589

P. sacculum Dale, name first published in Biourge, Monogr., La Cellule **33:** fasc. 1, p. 323; Col. Pl. XIII and Pl. XXIII, fig. 134. 1923. Miss Dale's organism was a *Scopulariopsis* described without name in Ann. Mycol. **12:** 59. 1914; above name assigned by Dale (E.) in Ann. Mycol. **24:** 1926.

P. salina (*Oospora*) Namyslowsky, 1913. In Biourge's Liste Onomastique, p. 105. 1923.

P. salmonicolor Raillo, in Centbl. f. Bakt. etc. (II) **78:** 522. 1929. Apparently a member of the *P. implicatum* series.

P. sanguifluum Sopp var. *lunzinense* v.Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 149. 1941. The single identifying character—swollen or vesicle-like conidiophore apices is too variable for separation as a variety.

Citromyces sanguifluus Sopp, in Monogr., pp. 115–117; Taf. XV, fig 105; Taf. XXII, fig. 3. 1912.

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Regarded as *P. roseo-purpureum* Dierckx 220

P. sanguifluus (*Citro.*) Sopp. In Biourge's Liste Onomastique, p. 105. 1923.

P. sanguineum Sopp, in Monogr., pp. 175–176; Taf. XIX, fig. 138; Taf. XXIII, fig. 24. 1912. Thom, The Penicillia, pp. 476–477. 1930. Regarded as probably synonymous with *P. purpurogenum* Stoll 636

P. saponis B. and Br. in Ann. Nat. Hist., 5th series, **7:** 130, Pl. III, fig. 3. 1881; No. 1913 of British fungi. Thom, The Penicillia, p. 588. 1930.

Syn. *Haplographium saponis* (B. and Br.) Sacc.

P. sartoryi Thom, in The Penicillia, p. 233. 1930. Regarded as approximating *P. citrinum* Thom, but transitional in the direction of ramigenous species of the Monoverticillata 349

P. scabrum Biourge, *nomen nudum*. A culture received from George Smith under this name represents a strain of *P. brevi-compactum* Dierckx.

P. schmidtii v.Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 166, fig. 20. 1941. Corresponds well enough with our description of *P. palitans* Westling to be included in that variable species.

P. schneggii Boas, in Myc. Centbl. **5:** 73–83. 1914. See also Centbl. f. Bakt. etc. (II) **44:** 695–696. 1916. Thom, The Penicillia, pp. 417–418. 1930. Regarded as probably synonymous with *P. granulatum* Bainier 546

P. schneggii (*Corem.*) Boas. In Biourge's Liste Onomastique, p. 105. 1923.

P. sclerotiorum van Beyma, in Zentbl. f. Bakt. etc. (II) **96:** 416–419, figs. 1 and 2. 1937 160

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P. scopulariopsis Sacc., in Sylloge **XXII:** 1275. 1913. Represents a name change from *Scopulariopsis communis* Bainier.

P. scortcum Takedo, Suematsu and Nakazawa, in J. Agr. Chem. Soc. Japan **10:** 95–121. 1934. Apparently represents a member of the *P. tardum* series. Our strain is distinguished by the usual production of conidia from *Cadophora*-like sterigmata 653

P. siderophilus Lieske, 1911. In Biourge's Liste Onomastique, p. 105. 1923.

P. siemaszki Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 487–488; Taf. 54. 1927. Some ramigenous form believed to approximate *P. charlesii* G. Smith.

P. silvatica (*Spic.*) Oudem. et Kon. In Biourge's Liste Onomastique, p. 105. 1923.

Coremium silvaticum Wehmer, in Ber. Deut. Botan. Gesell. **31:** 373–384. 1914. Synonym of *P. claviforme* Bainier 549

P. silvaticum Oud., in Arch. Neerlandaises des sc. Exactes et Nat., p. 289, tab. XXVII, figs. 1–4. 1902. Thom, The Penicillia, p. 571. 1930. From the description appears to probably represent *A. terreus* Thom.

P. silvaticum (*Corem.*) Wehmer. In Biourge's Liste Onomastique, p. 105. 1923.

P. silvaticum (Wehmer) Biourge, in Monogr., La Cellule **33:** fasc. 1, p. 105. 1923. Synonym of *P. claviforme* Bainier 549

P. silvaticum (Wehmer) Gaumann, in Vergl. Morph. Pilze, p. 177, fig. 113. 1926. Synonym of *P. claviforme* Bainier 551

P. simonarti Biourge is a MS name on a culture which proved to be *P. vermiculatum* Dang.

P. simplex Lindner, in Mikrosc.

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Betriebskontr., p. 315. 1901; Atlas Mikr. Grundl. Taf. **36:** Saccardo Syll. **XVIII:** 518. 1906. Seen often in culture. Not a *Penicillium*.

Syn. *Scopulariopsis simplex* (Lindner) Vuillemin, in Bul. Soc. Mycol. France **27:** 137–152. 1911. Thom, The Penicillia, p. 588. 1930.

Also described as *Catenularia fuliginea* Saito, and so cited in Lindner's Mikrosc. Betriebskontr. 5 aufl. 1909.

Known also as *Oospora vinosella* Sacc., Fung. Ital. t. 874. and *Torula vinosella* Sacc. Mich. I, p. 265. See also Sylloge **IV:** 20, 1886.

P. simplicissimum (Oud.) Thom, in The Penicillia, pp. 335–336, fig. 51. 1930 304

Syn. *Spicaria simplicissima* Oudemans, in Nederl. Kruidk. Arch. ser. 3, Vol. 2, p. 763. 1903; Jensen, Cornell Agr. Expt. Sta., Bul. 315, p. 493, fig. 127. 1912; Thom, The Penicillia, p. 335, fig. 51. 1930.

P. simplicissimum (Oud.) Thom var. *lunzinense* v.Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 156–157. 1941. The variety is described as having conidia elliptical instead of globose. Since this is the usual condition in the species no basis for the variety seems to exist.

P. sinicum Shih, in Sapporo Nat. Hist. Soc. Trans. **14:** 286–287, Pl. 12, fig. 3. 1936. Probably a member of the *P. frequentans* series 177

P. sitophilum Montagne in Ann. Sci. Nat., ser. II, **20:** 377, pl. 16, fig. 4. 1843. Thom, The Penicillia, p. 589. 1930.

Syn. *Monilia sitophila* (Mont.) Sacc., Sylloge **IV:** 35, 1886.

P. sitophilum (*Monilia*) Montagne. In Biourge's Liste Onomastique, p. 105. 1923.

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P. socium, credited to Plowright in Saccardo's Sylloge **2:** 468, 1883, as the conidial stage of *Hypomyces aureonitens* Tulasne; redescribed by Plowright in Grevillea **11:** 49, tab. 156, figs. b, d, f. 1882. This name is also listed by Grove in Jour. Bot. **23:** 165, 1885, as a synonym for *Gliocladium penicilloides* Corda. Thom, The Penicillia, p. 571. 1930. Not a true *Penicillium*.

P. solitum Westling, in Arkiv för Botanik **11:** 52, 65–67; figs. 3 and 47. 1911; Thom, The Penicillia, pp. 372–373. 1930 453

P. solitum Westling var. *lunzinense* v.Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 167. 1941. The variety is based upon smooth, globose conidia, 2 to 3μ. Without the describer's cultures the identity of his strain is doubtful, but it does fit the general concept of *P. solitum* as we understand this species.

P. soppi Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 476–477; Taf. 51. 1927. Thom, The Penicillia, p. 344. 1930 279

Citromyces sormanii Carbone, in Atti Ist. Bot. dell' Universita Pavia, Ser. II, 14, pp. 290–295, 321, Tav. XII, figs. 2, 3, 4. Probably represented a form approximating *P. citreo-viride* Biourge 218

P. sparsum Grev., in Scottish Crypt. Flora, **1:** pl. 58, fig. 2a and b, 1823. Thom, The Penicillia, p. 589. 1930. Not identifiable as a *Penicillium*.

Scop. sphaerospora Zach., in Österr. Bot. Zeitsch. **83:** 180–182, figs. 4 and 5. 1934 701

P. spiculisporum Lehman, in Mycologia **12:** 268–274, Pl. 19, figs. 1–37. 1920. See also Thom, The

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Penicillia, pp. 452–454. 1930; Emmons, Mycologia **27:** 135–136, figs. 3 and 16. 1935..... 589

P. spinulosum Thom, in U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, p. 76, fig. 32. 1910. In Thom, The Penicillia, pp. 183–184, fig. 21. 1930..... 180

P. spinulosum Thom var. *ramigena* v.Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 150. 1941. The name is applied to a very small monoverticillate form which showed rough, globose conidia, 3 to 4μ in diameter and branched conidiophores. Without the type culture or illustrations, the variety cannot be safely assigned.

P. staneri Biourge, in unpublished manuscript. Regarded as synonymous with *P. islandicum* Sopp on basis of culture received.

P. steckii Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 469–471, Taf. 50. 1927. Thom, The Penicillia, p. 255. 1930..... 350

P. stephaniae Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 451–452; Taf. 40. 1927. Thom, The Penicillia, pp. 395–396. 1930. Regarded as a synonym of *P. viridicatum* Westling..... 486

P. stilton Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 206–207; Col. Pl. V and Pl. VII, fig. 42. 1923. Thom, The Penicillia, p. 279. 1930..... 400

P. stipitatum Thom, in Emmons' Mycologia **27:** 138–141, figs. 6, 7, and 16. 1935..... 577

P. stoloniferum Thom, in U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, pp. 68–69, fig. 26. 1910; The Penicillia, pp. 292–294, figs. 41 and 42. 1930..... 412

P. striatum Raper and Fennell, in Mycologia **40:** 521–524, fig. 5. Williams, Cameron, and Williams, Food Research **6:** 69–73. 1941..... 606

P. suavolens Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 200–202; Col. Pl. V and Pl. VIII, fig. 4. 1923. Thom, The Penicillia, pp. 283–284. 1930. A member of the *P. roqueforti* series regarded as inseparable from the species *P. roqueforti* Thom..... 400

P. subcinereum Westling, in Arkiv för Botanik **11:** pp. 58, 137–139; figs. 41, 80. 1911. Apparently identifiable with *P. citreo-viride* Biourge..... 218

P. sublateritium Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 315–317; Col. Pl. X and Pl. XVI, fig. 92. 1923. Thom, The Penicillia, p. 222. 1930..... 203

P. subtile Berkeley, in Ann. and Mag. of Nat. Hist., Ser. 1, **6:** 437, Tab. XIV, fig. 25. 1841. Also Sacc., Sylloge **4:** 80. 1886. Thom, The Penicillia, p. 572. 1930. Not identifiable as a *Penicillium* from the description.

P. subtilis var. *ramosius* Grove, in Jour. of Bot. **23:** 165. 1885. Thom, The Penicillia, p. 572. 1930. No *Penicillium* with conidia 16 to 20 by 10μ has been reported since.

Citromyces subtilis Bainier and Sartory, in Bul. Soc. Mycol. France **28:** 46–47, Pl. II, figs. 5–7. 1912. Redescribed as *P. sartoryi* Thom, in The Penicillia, p. 233. 1930.

P. subviride v.Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 167–168, fig. 21. 1941. The measurements given suggest *P. camemberti* Thom.

P. sulfureum Sopp, in Monogr., pp. 172–173, Taf. XVII, fig. 120; Taf.

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XXIII, fig. 22. 1912. Thom, The Penicillia, pp. 482–483. 1930. Species known only from description; probably some member of the *P. purpurogenum* series. 636

P. sulfureum (?) Sopp, in Biourge, Monogr., La Cellule **33:** fasc. 1, pp. 241–242; Col. Pl. VII and Pl. XI, fig. 63. 1923. Thom, The Penicillia, p. 451. 1930. Regarded as probably a synonym of *P. miczynskii* Zaleski. 311

P. sumatrense v.Szilvinyi, in Archiv. f. Hydrobiologie Suppl. Bd. XIV; Tropische Binnengewasser Bd. VI, pp. 551–552. 1936. Regarded as a synonym of *P. corylophilum* Dierckx. 345

P. swiccickii Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 474–476; Taf. 51. 1927. Thom, The Penicillia, p. 353. 1930. Synonym of *P. nigricans* (Bainier) Thom. 329

P. syphiliticum Hallier, in Flora **51:** 295, 301, fig. 12. 1868, is described as a penicillate form assumed by *Coniothecium syphiliticum.* Thom, The Penicillia, p. 572. 1930. No one has since reported this species.

Coremium syphiliticum Hallier, in Flora **51:** 295, 301, fig. 16, 1868, is described as a form assumed by *Coniothecium syphiliticum.* Thom, The Penicillia, p. 572. 1930. No one has since reported this species.

P. szaferi Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 447–448, Taf. 38. 1927. Thom, The Penicillia, pp. 299–300. 1930. Believed to represent a synonym of *P. brevicompactum* Dierckx. 411

P. szulczewskii Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 502–504; Taf. 60. 1927. Probably based on a strain approximating *P. terlikowskii* Zaleski. Not further identified.

P. tabascens Westling, in Arkiv för Botanik **11:** 56, 100–102, figs. 20, 61. 1911. Thom, The Penicillia, p. 300. 1930. Believed to represent a synonym of *P. stoloniferum* Thom. 413

P. tannophagum Stapp and Bortels, in Zentbl. f. Bakt. etc. (II) **93:** 52. 1935. Belongs with *P. spinulosum* Thom. 185

P. tannophilum Stapp and Bortels, in Zentbl. f. Bakt. etc. (II) **93:** 52. 1935. Belongs with *P. spinulosum* Thom. 185

P. tardum Thom, in The Penicillia, pp. 485–486, fig. 84. 1930. 651

Citromyces tartricus Mazé and Perrier, in Ann. Inst. Pasteur **18:** 558–559. 1904. Member of the *P. frequentans-spinulosum* complex, but closer diagnosis impossible. 183

P. tenellum Cooke, in Grevillea **7:** 15, September 1875. Thom, The Penicillia, p. 573. 1930. Species not identifiable.

P. tenuis (*Gibellula*) (Heim) Vuillemin. In Biourge's Liste Onomastique, p. 106. 1923.

P. tenuissimum Corda, 1837. In Biourge's Liste Onomastique, p. 106. 1923.

P. terlikowskii Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 501–502; Taf. 59. 1927. Thom, The Penicillia, pp. 203–204. 1930. 231

P. terrestre Jensen, in Cornell Univ. Expt. Sta. Bul. 315, pp. 486–487, fig. 122. 1912; Thom, The Penicillia, pp. 371–372. 1930. 450

P. thermophilus (*Dactylomyces*) Sopp, in Biourge's Liste Onomastique, p. 106. 1923.

P. thomi Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 492–493; Taf. 56. 1927. Thom, The Penicillia, p. 366.

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1930. Not *P. thomii* Maire. Regarded as approximating *P. canescens* Sopp.

P. thomii Maire, in Bul. Soc. Hist. Nat. Afrique du Nord. **8:** pp. 189–192. 1917. Thom, U. S. Dept. Agr., Bur. Anim. Ind., Bul. 118, p. 78. 1910 (culture No. 29, discussed without name); also, The Penicillia, p. 173. 1930 156
Not *P. thomi* Zaleski, *q.v.*

P. tollensianus (*Citro.*) Wehmer, 1909. In Biourge's Liste Onomastique, p. 106. 1923.

P. toruloides Preuss, in Linnaea **25:** 728. 1852. Thom, The Penicillia, p. 573. 1930. Species not identifiable.

P. transversale Opiz (Streinz, 1862), in Biourge's Liste Onomastique, p. 106. 1923.

P. trzebinskii Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat., Ser. B, pp. 498–499; Taf. 58. 1927. In Thom, The Penicillia, p. 189. 1930 194

Citromyces tubcrifer Rostrup, in Bot. Tids. **29:** 32–41, illust. 1908. Rostrup's fungus probably represented a form approximating *Penicillium thomii* Maire.

Syn.? *P. tubifer* (*Citro.*) Rostrup, 1908, in Biourge's Liste Onomastique (Monograph, p. 106. 1923). Probably Biourge's usage represents a misspelling.

P. turbatum Westling, in Arkiv för Botanik **11:** pp. 54, 128–130, figs. 36 and 74. 1911. Thom, The Penicillia, p. 207. 1930 166

P. umbonatum Sopp, in Monogr., pp. 196–198; Taf. XXI, fig. 148; Taf. XXIII, fig. 40. 1912. Thom, The Penicillia, p. 255. 1930. Species known only from original description. Proper assignment uncertain. Possibly approximates *P. corylophilum* Dierckx.

P. uredinicolum Hulea, in Bul. Sect. Sci. Acad. Roum. (Bucharest) **22:** 16, fig. 14. 1939. Name applies to new species which was inadequately described and illustrated. Isolated from the aecidia of *Puccinia* and *Mellampsora* species. Possibly one of the *Penicillium citrinum* series.

P. urticae Bainier, in Bul. Soc. Mycol. France **23:** 15–16; Pl. IV, figs. 1–5. 1907. Thom, The Penicillia, pp. 418–419. 1930. . . 534

P. vanillae Bouriquet, in Bul. Acad. Malgache, N. S., **24:** 65–77, 2 Col. Pls. 1941. Correct placement of species in doubt; inadequately described and no figure of microscopic details presented. Author suggests Thom's Asymmetrica-Velutina (1930).

P. variabile Sopp, in Monogr., pp. 169–171; Taf. XVIII, fig. 124; Taf. XXIII, fig. 27. 1912. Thom, The Penicillia, p. 477. 1930 642

P. variabile Wehmer, in Mycol. Centbl. **2:** 195–203. 1913; Thom, The Penicillia, pp. 410–411. 1930. Synonym of *P. expansum* Link 516

P. variabile Westling. In Biourge's Liste Onomastique, p. 106. 1923; Thom, The Penicillia, p. 411. 1930.

P. varians Munk-Wehmer, 1913. In Biourge's Liste Onomastique, p. 106. 1923. Thom (1930, p. 411) considered this as probably a misprint for *P. variabile* Wehmer.

P. varians Smith, in Brit. Mycol. Soc. Trans. **18:** 89–90; Pl. IV, fig. 3. 1933 625

P. varians v. Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 168, fig. 22. 1941. The describer's sketch, together with his descriptive notes, would seem to ally this with the *P. janthinellum* series. The same name had been previously used by George Smith

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for a species belonging to the *P. funiculosum* series.

Paccilomyces varioti Bainier, in Bul. Soc. Mycol. France **23:** 26, Pl. VII. 1907 691

Syn. *P. divaricatum* Thom, *q.v.* *Spicaria divaricata* (Thom) Gilman and Abbott, in Iowa State College Jour. Sci. **1:** 301. 1927.

P. varioti (*Paecilomyces*) Bainier, 1907. In Biourge's Liste Onomastique, p. 106. 1923.

P. velutinum v. Beyma, in Zentbl. f. Bakt. etc. (II) **91:** 352–354, fig. 6. 1935 250

Scop. venerei Greco, in Origine des tumeurs et observationes de mycoses, pp. 709–721, p. 823, Pl. XXI and XXVIII, figs. 437–442, Buenos Aires. 1916 704

P. ventruosum Westling, in Arkiv för Botanik **11:** 57, 112–114, figs. 26, 67. 1911. Thom, The Penicillia, pp. 415–416. 1930. Synonym of *P. italicum* Wehmer 529

P. vermiculatum Dangeard, in Le Botaniste **10:** 123–139, Pls. 16–20. See also Emmons, Mycologia **27:** 136–137, figs. 4, 5, and 16. 1935 580

P. vermoeseni Biourge, in Monogr., La Cellule **33:** fasc. 1, p. 230; Pl. XXIII, fig. 137. 1923.

Syn. *G. vermoeseni* (Biourge) Thom, in The Penicillia, pp. 502–503. 1930 680

P. vermoeseni (*Corem.*) Biourge, 1923. In Biourge's Liste Onomastique, p. 106. 1923.

P. verrucosum Dierckx, in Soc. Scientifique Bruxelles **25:** 88. 1901; Biourge, Monogr., La Cellule **33:** 123–126; Col. Pl. I and Pl. II, fig. 7. 1923. Thom, The Penicillia, p. 395. 1930. Member of the *P. viridicatum* series with conidiophores conspicuously roughened 486

P. verruculosum Peyronel, in I germi atmosferici dei funghi con micelio, p. 22, Padova. 1913.

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Thom, The Penicillia, p. 474. 1930 621

P. versicolor (*Citrom.*) Wehmer. In Biourge's Liste Onomastique, p. 106. 1923.

P. verticillatum Corda, in Icones I, p. 21, table 6, fig. 281. 1837; Thom, The Penicillia, p. 589. 1930. In Biourge's Liste Onomastique as *P.* (*Spic.*) *verticillatum* (Corda) Harz.

P. verticilliferum Spegazzini, in Physis **7:** no. 23, p. 18. 1923. Thom, The Penicillia, p. 573. 1930. No one has rediscovered a *Penicillium* with the complex fruiting mass described.

P. verticillioides (*Spicaria*) Fron, 1911. In Biourge's Liste Onomastique, p. 106. 1923.

P. vesiculosum Bainier, in Bul. Soc. Mycol. France **23:** 10–12; Pl. II, figs. 1–8. 1907. Thom, The Penicillia, p. 287, fig. 39. 1930. The structures described and illustrated by Bainier appear to to be pathological. The species is believed to have been based upon some aberrant member of the *P. roqueforti* series 400

P. vinaceum Gilman and Abbott, in Iowa State College Jour. Sci. **1:** No. 3, p. 299, fig. 34. 1927. Thom, The Penicillia, pp. 195–196, fig. 23. 1930 234

P. viniferum Sakaguchi, in Zentbl. f. Bakt. etc. (II) **100:** 302–307. 1939. Species based upon a *Paecilomyces* approximating *P. varioti* Bain 690

Spicaria violacea Abbott, in Iowa State College Jour. Sci. **1:** 26, fig. 3. 1926; see also, Gilman and Abbott, Iowa State College Jour. Sci. **1:** 301. 1926; Thom, The Penicillia, p. 335. 1930 288

Acaulium violaceum Sopp, in Monogr., pp. 56–60, Taf. IV and VIII, figs. 70–74. 1912. Pos-

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sibly represented *S. brevicaulis* (Sacc.) Bainier.

P. violaceum Biourge, in Semal. O. 1897. Thom, The Penicillia, p. 589. 1930. Included in Biourge's Liste Onomastique, Monograph, p. 106. 1923, but never described or figured.

P. virellum Peyronel, in I germi atmosferici dei funghi con micelio, p. 22, Padova. 1913. Thom, The Penicillia, p. 573. 1930. Species known only from description. Suspected of representing *P. oxalicum* Currie and Thom.

P. virescens Bainier, in Bul. Soc. Myc. France **23:** 12, Pl. II, figs. 9–12. 1907; Thom, The Penicillia, p. 265. 1930. Species not subsequently identified; probably near *P. notatum* Westling.

P. virescens Sopp, in Monogr., pp. 157–159, Taf. XVII, fig. 121; Taf. XXII, figs. 4 and 5. 1912. Thom, The Penicillia, p. 283. 1930. Not *P. virescens* Bainier (1907). Sopp's description clearly indicates that he had some strain of *P. roqueforti* Thom.

P. viride Fresenius, in Beitr. z. Myk., pp. 21–22, Taf. III, figs. 16–19. 1851–1853. Thom, The Penicillia, p. 589. 1930. Probably some *Cladosporium*.

P. viride Rivolta, in Parass. Veget., p. 453, Tav. VI, fig. 154a. 1873. Thom, The Penicillia, p. 590, 1930. Probably some *Cladosporium*.

P. viride-albo v.Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 151, fig. 7. 1941. A culture marked *P. viride-albo* from CBS (originally from Janke) proved to be some strain of *Aspergillus versicolor* (Vuill.) Tiraboschi.

P. viride-varians Chaudhuri and Sachar, in Ann. Mycol. **32:** 98, Pl.1. 1934. From the inadequate description given, the species appears to belong in the Divaricata possibly approximating *P. nalgiovensis* Laxa.

P. viridiacum Westling. Misprint for *P. viridicatum* Westling in Wehmer, Mycol. Centbl. **2:** 201. 1913.

P. viridicatum Westling, in Arkiv för Botanik **11:** 53, 88–90, figs. 14 and 56. 1911. Thom, The Penicillia, p. 394. 1930 482

P. viridicatum ? Westling, Dale. In Biourge's Liste Onomastique, p. 106. 1923.

P. viridi-dorsum Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 306–307; Col. Pl. VIII and Pl. XIII, fig. 75. 1923. Regarded as *P. spinulosum* Thom 185

Citromyces virido-albus Sopp, in Monogr., pp. 131–132; Taf. XIII, fig. 98; Taf. XXII, fig. 12. 1912. Regarded as *P. purpurrescens* (Sopp) n. comb. 180

P. virido-bruneum Sopp, in Monogr., pp. 200–201, Taf. XX, fig. 150; Taf. XXIII, fig. 42. 1912; see Thom, The Penicillia, p. 456. 1930. Species not identifiable; not subsequently reported. Doubtfully a member of the *P. luteum* series.

P. virido-bruneum Sopp var. *lunzinense* v.Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 161. 1941. No one since Sopp has ventured to identify *P. virido-bruneum*. The description of the variety fails to supply adequate bases for identification.

P. viridum Sopp, in Monogr., pp. 198–200, Taf. XIX, fig. 137; Taf. XXIII, fig. 41. 1912. Thom, The Penicillia, p. 590. 1930. Probably some member of the *Aspergillus restrictus* series.

Coremium vulgare Corda, in Prachtflora, p. 54, Pl. XXV, figs. 3 and 4, 17–21. 1839. Possibly repre-

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sents *P. claviforme* Bainier in part 551

P. waksmani Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 468–469; Taf. 49. 1927. Thom, The Penicillia, pp. 230–231. 1930..... 246

P. (Citrom.) wallandi v.Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 151–152, fig. 8. 1941. The species is described in terms which place it in the *P. spinulosum* series near *P. purpurrescens* Sopp.

P. weidemanni Westling, in Biourge, Monogr., La Cellule **33:** fasc. 1, p. 204, 1923. This usage represents an error in citation of *P. roqueforti* var. *wiedemanni* Westling made by Biourge.

P. weidemanni Westling, var. *fuscum* Arnaudi, in Boll. Ist. Sieroterapico Milanese **6:** fasc. 1, pp. 18–27. 1927. Thom, The Penicillia, p. 282. 1930. Arnaudi described this strain as having slight color differences in culture from other members of the *P. roqueforti* series.

P. westlingi Zaleski, in Bul. Acad. Polonaise Sci.: Math. et Nat. Ser. B, pp. 473–474, Taf. 54. 1927. Thom, The Penicillia, p. 253. 1930. Believed to be a synonym of *P. waksmani* Zaleski.

P. westlingi Zaleski var. *lunzinense* v.Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 171–172. 1941. This species is regarded as synonymous with *P. waksmani* Zaleski. Doubtful if bases for recognition of variety exist.

P. wortmanni Klöcker, in Compt. Rend. Laborat. Carlsberg. **6:** 100. 1903. See Biourge, Monogr., La Cellule **33:** fasc. 1, p. 244. 1923; Thom, The Penicillia, pp. 449–450. 1930; and Emmons, Mycologia **27:** 133–135, figs. 1 and 16. 1935..... 583

P. wuchangense Shih, in Trans. Sapporo Nat. Hist. Soc. **14:** 287. 1936. Shih thought this species to be near *P. restrictum* but showing colonies bluish green and conidia smooth. A monoverticillate form suggesting *P. decumbens* Thom.

P. wurceburgense in Biourge, Monogr., La Cellule **33:** fasc. 1, Col. Pl. V and Pl. VIII, fig. 47. 1923. Thom, The Penicillia, p. 247. 1930. Name proposed, without description, for a culture distributed by Kral in 1913 as *P. olivaceum* Wehmer from Würzburg. Biourge suggested the name since Thom (1910) had abandoned *P. olivaceum*, and since Biourge wished to retain the name *P. digitatum* Sacc. for cultures found on fruits from the South. Thom, (1930) regarded it as probably similar to *P. oxalicum* Currie and Thom.

P. zaleskii v.Szilvinyi, in Zentbl. f. Bakt. etc. (II) **103:** 172, fig. 24. 1941. The describer placed his organism in the series with *P. chrysogenum*, but his drawing does not correspond with this placement. Species believed to approximate *P. corylophilum* Dierckx.

P. zukalii Biourge, in Monogr., La Cellule **33:** fasc. 1, pp. 239–240; Col. Pl. VII and Pl. XI, fig. 61. 1923. Thom, The Penicillia, p. 460. 1930. Identity uncertain. Described as a coremiform species; rediscussed (La Cellule **36:** 445–454, Pl. I. 1925) as producing perithecia and sclerotia. Cultures distributed by Biourge under this name proved to be *P. brefeldianum* Dodge..... 154

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